

Neotropical Monogenoidea. 29. Ancyrocephalinae (Dactylogyridae) of Piranha and Their Relatives (Teleostei, Serrasalminae) from Brazil: Species of *Amphithecium* Boeger and Kritsky, 1988, *Heterothecium* gen. n. and *Pithanothecium* gen. n.

DELANE C. KRITSKY,¹ WALTER A. BOEGER,² AND MICHEL JÉGU³

¹ College of Health Professions, Idaho State University, Pocatello, Idaho 83209 (e-mail: kritdela@isu.edu),

² Departamento de Zoologia, Universidade Federal do Paraná, Caixa Postal 19020, Curitiba, Paraná 81530, Brazil, and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (e-mail: wboeger@bio.ufrpr.br), and

³ Antenne ORSTOM, Laboratoire d'Ichtyologie, MNHN, 43 rue Cuvier 75231 Paris Cedex, France (e-mail: jegu@mnhn.fr)

ABSTRACT: Fifteen species (9 new) of *Amphithecium*, 2 new species of *Heterothecium*, and 2 species of *Pithanothecium* are described and/or reported from the gills of 14 species of Serrasalminae from the Brazilian Amazon: *Amphithecium calycinum* Boeger and Kritsky, 1988, *A. brachycirrum* Boeger and Kritsky, 1988, *A. camelum* Boeger and Kritsky, 1988, and *A. catalaoensis* Boeger and Kritsky, 1988, from *Pygocentrus nattereri*; *Amphithecium diclonophallum* sp. n. from *Pristobrycon* sp., *Serrasalmus compressus*, *S. elongatus*, *S. gouldingi*, *S. rhombeus*, and *Serrasalmus* sp. (2 of Jégu); *Amphithecium falcatum* Boeger and Kritsky, 1988, from *Pristobrycon* sp., *Pygocentrus nattereri*, *Serrasalmus compressus*, *S. elongatus*, *S. gouldingi*, *S. manuelli*, *S. rhombeus*, *S. spilopleura*, *Serrasalmus* sp. (2 of Jégu), and *Serrasalmus* sp. (2n = 58); *Amphithecium junki* Boeger and Kritsky, 1988, from *Pygocentrus nattereri* and *Serrasalmus rhombeus*; *Amphithecium microphallum* sp. n. from *Pygocentrus nattereri* and *Serrasalmus* sp. (2n = 58); *Amphithecium minutum* sp. n. from *Pristobrycon eigenmanni*, *Pristobrycon* sp., *Serrasalmus gouldingi*, and *S. spilopleura*; *Amphithecium muricatum* sp. n. from *Pristobrycon eigenmanni*, *Serrasalmus rhombeus*, and *Serrasalmus* sp. (2 of Jégu); *Amphithecium pretiosum* sp. n. from *Pristobrycon* sp., *Serrasalmus gouldingi*, and *S. manuelli*; *Amphithecium prodotum* sp. n. from *Catopryon mento* and *Pristobrycon striolatus*; *Amphithecium speirocamarotum* sp. n. from *Serrasalmus elongatus*; *Amphithecium unguiculum* sp. n. from *Serrasalmus spilopleura*; *Amphithecium verecundum* sp. n. from *Pristobrycon eigenmanni* and *Serrasalmus* sp. (2 of Jégu); *Heterothecium globatum* sp. n. from *Serrasalmus gouldingi*; *Heterothecium dicrophallum* sp. n. from *Catopryon mento*; *Pithanothecium piranhus* (Mizelle and Price, 1965) comb. n. from *Catopryon mento*, *Pristobrycon striolatus*, *Pygocentrus nattereri*, and *Pygopristis denticulata*; and *Pithanothecium amazonensis* (Mizelle and Price, 1965) comb. n. from *Catopryon mento*, *Pristobrycon striolatus*, and *Pygopristis denticulata*. The diagnosis of *Amphithecium* is emended, and 2 new genera are proposed. *Heterothecium* gen. n. characterized by species having a sinistrodorsal vaginal pore, a sclerotized vaginal vestibule, a male copulatory organ with 2 rami, and simple distal termination of the articulation process of the accessory piece. Characters distinguishing *Pithanothecium* gen. n. include presence of a sclerotized vaginal vestibule opening on the dextrolateral surface of the trunk and a distally blunt articulation process of the accessory piece extending past the tip of the distal rod. *Cleidodiscus piranhus* Mizelle and Price, 1965, and *C. amazonensis* Mizelle and Price, 1965, are transferred to *Pithanothecium*.

KEY WORDS: Monogenoidea, Dactylogyridae, Ancyrocephalinae, *Amphithecium*, *Heterothecium* gen. n., *Pithanothecium* gen. n., *Amphithecium brachycirrum*, *Amphithecium calycinum*, *Amphithecium camelum*, *Amphithecium catalaoensis*, *Amphithecium diclonophallum* sp. n., *Amphithecium falcatum*, *Amphithecium junki*, *Amphithecium microphallum* sp. n., *Amphithecium minutum* sp. n., *Amphithecium muricatum* sp. n., *Amphithecium pretiosum* sp. n., *Amphithecium prodotum* sp. n., *Amphithecium speirocamarotum* sp. n., *Amphithecium unguiculum* sp. n., *Amphithecium verecundum* sp. n., *Heterothecium dicrophallum* sp. n., *Heterothecium globatum* sp. n., *Pithanothecium amazonensis* comb. n., *Pithanothecium piranhus* comb. n., Serrasalminae, *Catopryon mento*, *Pristobrycon eigenmanni*, *Pristobrycon striolatus*, *Pristobrycon* sp., *Pygocentrus nattereri*, *Pygopristis denticulata*, *Serrasalmus compressus*, *Serrasalmus elongatus*, *Serrasalmus gouldingi*, *Serrasalmus manuelli*, *Serrasalmus rhombeus*, *Serrasalmus spilopleura*, *Serrasalmus* sp., Amazon Basin, Brazil.

This paper represents the second of 4 contributions dealing with Ancyrocephalinae from the gills of Amazonian Serrasalminae (see Kritsky et al.,

1996, in press a, b). It includes 15 species of *Amphithecium* Boeger and Kritsky, 1988, 2 of *Heterothecium* gen. n., and 2 of *Pithanothecium* gen. n.

Materials and Methods

Methods of collection of hosts and their parasites and of mounting, illustration, and measurement of helminths are as described by Kritsky et al. (1986, 1996). All measurements are in micrometers; the mean is followed by the range and number of specimens measured in parentheses; length of the accessory piece is that of the distal rod. Numbering (distribution) of hook pairs follows that recommended by Mizelle (1936; see Mizelle and Price, 1963). Type and voucher specimens of helminths are deposited in the parasite collections of Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; the United States National Museum (USNPC), Beltsville, Maryland; and the University of Nebraska State Museum (HWML), as indicated in the respective descriptions or accounts of species. For comparative purposes, the following specimens were examined: *Cleidodiscus amazonensis* Mizelle and Price, 1965, holotype (USNPC 60462), paratype (HWML 21289), and *C. piranhus* Mizelle and Price, 1965, holotype (USNPC 60463), paratype (HWML 21290).

Presumed undescribed hosts have been provisionally identified by M.J. as *Pristobrycon* sp., *Serrasalmus* sp. (2 of Jégu), and *Serrasalmus* sp. (2n = 58). Representative specimens of provisionally identified host taxa are deposited in the ichthyology collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

Taxonomic Account

Class Monogenoidea Bychowsky, 1937
Order Dactylogyridea Bychowsky, 1937
Dactylogyridae Bychowsky, 1933
Ancyrocephalinae Bychowsky, 1937
***Amphithecium* Boeger and Kritsky, 1988**

EMENDED DIAGNOSIS: Body fusiform or flattened dorsoventrally; comprising cephalic region, trunk, peduncle, haptor. Tegument thin, smooth, scaled or papillate. Two terminal, 2 bilateral cephalic lobes; head organs, unicellular cephalic glands present. Eyes 4, anterior pair infrequently absent; granules elongate ovate. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus short; intestinal ceca 2, confluent posterior to testis, lacking diverticula. Gonads intercecal, overlapping; testis dorsal to germarium. Vas deferens looping left intestinal cecum; seminal vesicle a sigmoid dilation of the vas deferens. Two prostatic reservoirs; prostates comprising 2 bilateral glandular areas lying dorsal to anterior portions of ceca. Genital pore midventral near level of cecal bifurcation. Copulatory complex comprising an accessory piece articulating to base of tubular copulatory organ by variable, flexible proximal articulation process. Two bilateral vaginae, nonsclerotized, di-

lated; each looping respective intestinal cecum, opening on dorsolateral surfaces; seminal receptacle usually absent. Haptor subhexagonal, with pairs of dorsal and ventral anchor/bar complexes, 7 pairs of similar hooks with ancyrocephaline distribution. Hooks similar; each with delicate point, truncate protruding thumb, expanded shank comprising 2 subunits; proximal subunit variable in length between hook pairs. FH loop extending to union of shank subunits. Parasites of gills of Serrasalminae.

TYPE SPECIES: *Amphithecium calycinum* Boeger and Kritsky, 1988, from *Pygocentrus nattereri*.

OTHER SPECIES: *Amphithecium brachycirrum* Boeger and Kritsky, 1988, from *Pygocentrus nattereri*; *A. camelum* Boeger and Kritsky, 1988, from *P. nattereri*; *A. catalaoensis* Boeger and Kritsky, 1988, from *P. nattereri*; *A. diclonophallum* sp. n. from *Pristobrycon* sp., *Serrasalmus elongatus*, *S. gouldingi*, *S. rhombeus*, and *Serrasalmus* sp. (2 of Jégu); *A. falcatum* Boeger and Kritsky, 1968, from *Pristobrycon* sp., *Pygocentrus nattereri*, *S. elongatus*, *S. gouldingi*, *S. manuelli*, *S. rhombeus*, *S. spilopleura*, *Serrasalmus* sp. (2 of Jégu), and *Serrasalmus* sp. (2n = 58); *A. junki* Boeger and Kritsky, 1988, from *Pygocentrus nattereri* and *S. rhombeus*; *A. microphallum* sp. n. from *P. nattereri* and *Serrasalmus* sp. (2n = 58); *A. minutum* sp. n. from *Pristobrycon eigenmanni*, *Pristobrycon* sp., *S. gouldingi*, and *S. spilopleura*; *A. muricatum* sp. n. from *P. eigenmanni*, *S. rhombeus*, and *Serrasalmus* sp. (2 of Jégu); *A. pretiosum* sp. n. from *Pristobrycon* sp., *Serrasalmus gouldingi*, and *S. manuelli*; *A. prodotum* sp. n. from *Catoprion mento* and *P. striolatus*; *A. speirocamarotum* sp. n. from *S. elongatus*; *A. unguiculum* sp. n. from *S. spilopleura*; and *A. verecundum* sp. n. from *P. eigenmanni* and *Serrasalmus* sp. (2 of Jégu).

REMARKS: Boeger and Kritsky (1988) characterized *Amphithecium* by specimens possessing bilateral nonsclerotized vaginae opening dorsolaterally, a biramous copulatory organ, overlapping gonads, an accessory piece articulated to the base of the copulatory organ, and hook shanks comprising 2 subunits. Of these, the features of the vaginae apparently represent the only synapomorphies. In their phylogenetic hypothesis, Boeger and Kritsky (1988) considered double vaginae to be a synapomorphy for the clade containing *Amphithecium*, *Notothe-*

cium, and *Notozothecium* with the single vaginal branches of members of the latter 2 genera being derived. However, these authors indicated that consideration of bilateral vaginae a synapomorphy for the clade of *Amphithecium* species was equally parsimonious. One other ancyrocephaline genus, *Calpidothecioides*, is characterized by members with double vaginae (Kritsky et al., in press a). In species of *Calpidothecioides*, the dextral vagina opens middorsally, and the sinistral branch opens on the left margin of the body.

***Amphithecium calycinum* Boeger and Kritsky, 1988 (Figs. 1–9)**

RECORDS: *Pygocentrus nattereri*: Rio Uatuma, Lago Tapaná, near Santana, Amazonas (3 November 1989); Furo do Catalão, Manaus, Amazonas (26, 27 November 1984).

PREVIOUS RECORDS: *Pygocentrus nattereri* (type host): Furo do Catalão, Manaus, Amazonas; Ilha da Marchantaria, Rio Solimões, Manaus, Amazonas; Rio Pacaás-Novos, Guajará-Mirim, Rondônia; Rio Mamoré, Surpresa, Rondônia; Rio Guaporé, Surpresa, Rondônia (type locality); Rio Guaporé, Costa Marques, Rondônia (all Boeger and Kritsky, 1988).

SPECIMENS STUDIED: Forty-three vouchers, USNPC 85786, 85787.

MEASUREMENTS: Body length 287 (231–319; $n = 9$), greatest width 101 (80–122; $n = 9$); haptoral length 56 (43–63; $n = 9$), width 76 (64–85; $n = 8$); pharyngeal diameter 17 (16–19; $n = 9$); ventral anchor length 29 (27–31; $n = 24$), base width 13 (11–14; $n = 20$); dorsal anchor length 30 (29–33; $n = 23$), base width 13 (12–14; $n = 16$); ventral bar 28 (26–30; $n = 5$), dorsal bar 24 (23–26; $n = 5$) long; hook pair 1–16–17 ($n = 11$), pairs 2, 6–17 (15–20; $n = 31$), pairs 3, 4, 7–23 (21–25; $n = 50$), pair 5–13–14 ($n = 16$) long; copulatory organ length 32 (26–35; $n = 23$), accessory piece length 21 (17–24; $n = 19$); testis 61 (51–72; $n = 6$) long, 26 (23–31; $n = 6$) wide; germarium 62 (48–91; $n = 8$) long, 25 (19–28; $n = 8$) wide.

REMARKS: *Amphithecium calycinum* was adequately described as the type species for the genus by Boeger and Kritsky (1988). Our specimens do not differ significantly in morphology and size from those originally reported. The species is apparently restricted to *Pygocentrus nattereri* and is distinguished by having a loosely

coiled or twisted primary ramus and broad secondary ramus of the copulatory organ.

***Amphithecium brachycirrum* Boeger and Kritsky, 1988 (Figs. 10–19)**

RECORDS: *Pygocentrus nattereri*: Rio Uatuma, Lago Tapaná, near Santana, Amazonas (3 November 1989); Furo do Catalão, Manaus, Amazonas (26, 27 November 1984).

PREVIOUS RECORDS: *Pygocentrus nattereri* (type host): Furo do Catalão, Manaus, Amazonas (type locality); Ilha da Marchantaria, Rio Solimões, Manaus, Amazonas; Rio Pacaás-Novos, Guajará-Mirim, Rondônia; Rio Mamoré, Surpresa, Rondônia; Rio Guaporé, Surpresa, Rondônia; Rio Guaporé, Costa Marques, Rondônia (all Boeger and Kritsky, 1988).

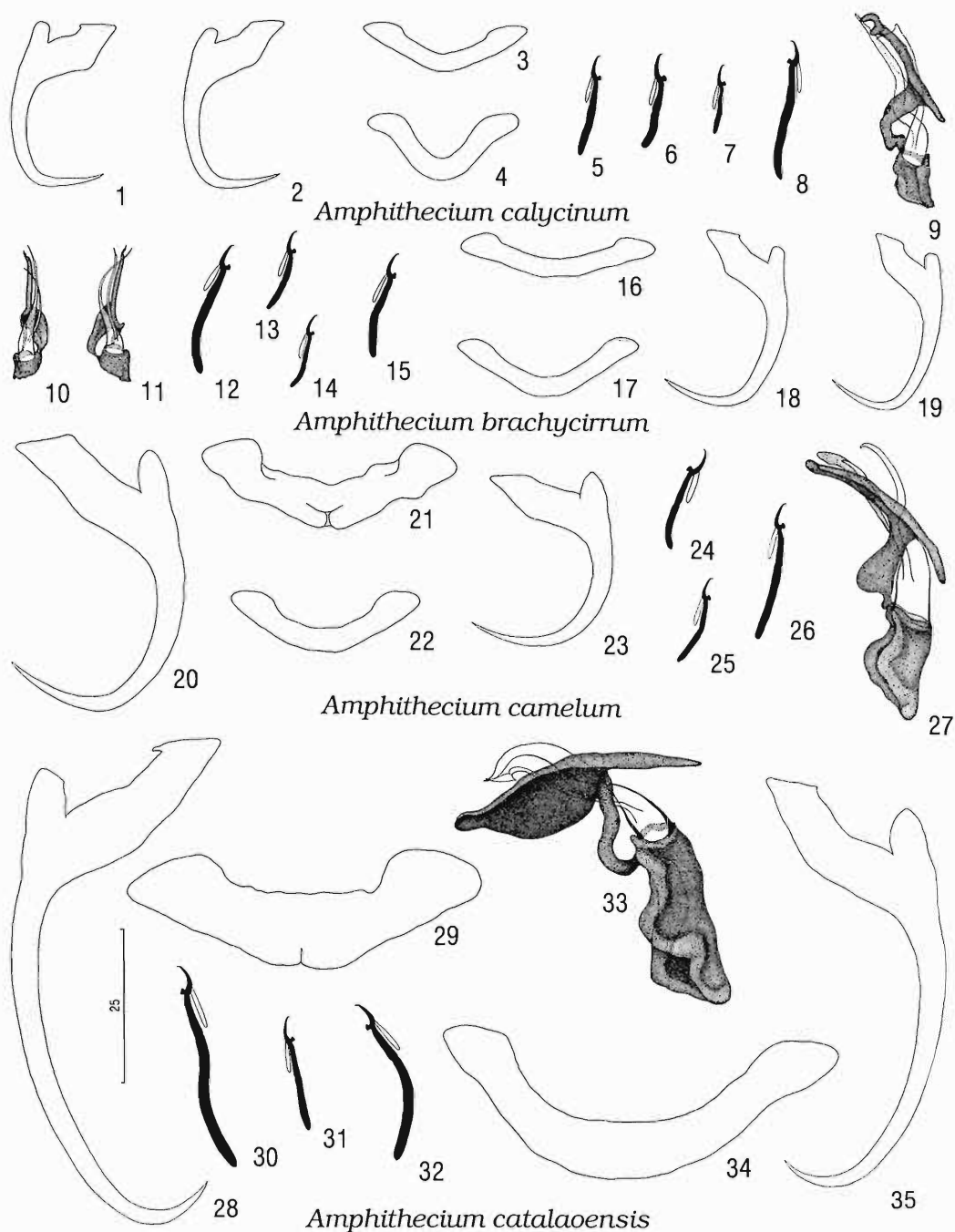
SPECIMENS STUDIED: Twenty-three vouchers, USNPC 85788, 85789.

MEASUREMENTS: Body length 260 (248–272; $n = 2$), greatest width 112 ($n = 2$); haptoral length 49 (46–52; $n = 2$), width 69 (62–75; $n = 2$); pharyngeal diameter 17 ($n = 2$); ventral anchor length 28 (26–31; $n = 20$), base width 12 (11–14; $n = 19$); dorsal anchor length 28 (26–30; $n = 13$), base width 12 (10–13; $n = 8$); ventral bar 30 (27–32; $n = 2$), dorsal bar 27 (25–29; $n = 2$) long; hook pair 1–15 (14–16; $n = 5$), pairs 2, 6–18 (17–20; $n = 22$), pairs 3, 4, 7–22 (21–24; $n = 37$), pair 5–13–14 ($n = 11$) long; copulatory organ length 21 (20–24; $n = 13$), accessory piece length 16 (15–17; $n = 12$); testis 53 ($n = 1$) long, 29 ($n = 1$) wide; germarium 63 (54–72; $n = 2$) long, 26 (24–28; $n = 2$) wide.

REMARKS: *Amphithecium brachycirrum* is apparently restricted to *Pygocentrus nattereri*. Our specimens do not differ significantly from the original description except that the distal rod of the accessory piece extends from a level of the base to the tip of the primary ramus of the copulatory organ. Boeger and Kritsky (1988) missed the proximal extension of the distal rod from its submedial twist. In some specimens, the proximal extension is difficult to observe when it lies over or below the articulation process of the accessory piece.

***Amphithecium camelum* Boeger and Kritsky, 1988 (Figs. 20–27)**

RECORDS: *Pygocentrus nattereri*: Rio Uatuma, Lago Tapaná, near Santana, Amazonas (3 November 1989); Furo do Catalão, Manaus,



Figures 1–35. Sclerotized structures of *Amphithecium* spp. 1–9. *Amphithecium calycinum* Boeger and Kritsky, 1988. 1. Ventral anchor. 2. Dorsal anchor. 3. Ventral bar. 4. Dorsal bar. 5. Hook pair 2. 6. Hook pair 1. 7. Hook pair 5. 8. Hook pair 7. 9. Copulatory complex (ventral view). 10–19. *Amphithecium brachycirrum* Boeger and Kritsky, 1968. 10, 11. Copulatory complexes (dorsal views). 12. Hook pair 7. 13. Hook pair 1. 14. Hook pair 5. 15. Hook pair 2. 16. Ventral bar. 17. Dorsal bar. 18. Ventral anchor. 19. Dorsal bar. 20–27. *Amphithecium camelum* Boeger and Kritsky, 1968. 20. Ventral anchor. 21. Ventral bar. 22. Dorsal bar. 23. Dorsal anchor. 24. Hook pair 1. 25. Hook pair 5. 26. Hook pair 7. 27. Copulatory complex (ventral view). 28–35. *Amphithecium catalaoensis* Boeger and Kritsky, 1968. 28. Ventral anchor.

Amazonas (26, 27 November 1984); Ilha da Marchantaria, Rio Solimões, Manaus, Amazonas (25 November 1984).

PREVIOUS RECORDS: *Pygocentrus nattereri* (type host): Furo do Catalão, Manaus, Amazonas; Ilha da Marchantaria, Rio Solimões, Manaus, Amazonas (type locality); Rio Pacaás-Novos, Guajará-Mirim, Rondônia; Rio Mamoré, Surpresa, Rondônia; Rio Guaporé, Surpresa, Rondônia; Rio Guaporé, Costa Marques, Rondônia (all Boeger and Kritsky, 1988).

SPECIMENS STUDIED: Nineteen vouchers, USNPC 85790, 85791, 85792.

MEASUREMENTS: Body length 456 (387–489; $n = 8$), greatest width 180 (100–218; $n = 9$); haptoral length 67 (56–75; $n = 9$), width 90 (67–103; $n = 9$); pharyngeal diameter 25 (22–26; $n = 9$); ventral anchor length 46–47 ($n = 7$), base width 23 (21–26; $n = 7$); dorsal anchor length 30 (29–31; $n = 5$), base width 19 (15–20; $n = 5$); ventral bar 42 (39–45; $n = 7$), dorsal bar 34 (31–37; $n = 8$) long; hook pairs 1, 5–19 (17–21; $n = 8$), pairs 2, 6–22 (20–23; $n = 9$), pairs 3, 7–24 (22–26; $n = 8$), pair 4–28–29 ($n = 4$) long; copulatory organ 48 (44–55; $n = 9$) long, accessory piece 33 (31–38; $n = 8$) long; testis 106 (79–147; $n = 4$) long, 48 (36–74; $n = 4$) wide; germarium 123 (98–155; $n = 8$) long, 56 (33–80; $n = 7$) wide.

REMARKS: *Amphithecium camelum* is known only from *Pygocentrus nattereri*. Present specimens do not differ significantly from the original description. Boeger and Kritsky (1988) reported 2 forms of this species from distant locations within the Amazon Basin based on comparative morphology of the copulatory organ. The preceding specimens are included in *Amphithecium camelum* forma amazonas, because both rami of the copulatory organ terminate acutely.

***Amphithecium catalaoensis* Boeger and Kritsky, 1988 (Figs. 28–35)**

RECORD: *Pygocentrus nattereri*: Rio Uatumã, Lago Tapaná, near Santana, Amazonas (3 November 1989).

PREVIOUS RECORD: *Pygocentrus nattereri* (type host): Furo do Catalão, Manaus, Amazonas (type locality) (Boeger and Kritsky, 1988).

SPECIMENS STUDIED: One voucher, USNPC 85793.

MEASUREMENTS: Ventral anchor length 79 ($n = 1$), base width 31 ($n = 1$); dorsal anchor length 71 ($n = 1$), base width 26 ($n = 1$); ventral bar 60 ($n = 1$), dorsal bar 65 ($n = 1$) long; hook pairs 1, 6–24–25 ($n = 3$), pair 2–28 ($n = 2$), pair 3–32–33 ($n = 2$), pair 4–35 ($n = 1$), pair 5–20–21 ($n = 2$), pair 7–30 ($n = 1$) long; copulatory organ length 56 ($n = 1$), accessory piece length 41 ($n = 1$).

REMARKS: Only a single specimen was found on *Pygocentrus nattereri* from central Amazonia. It was similar to those collected by Boeger and Kritsky (1988) from this host in the Furo do Catalão.

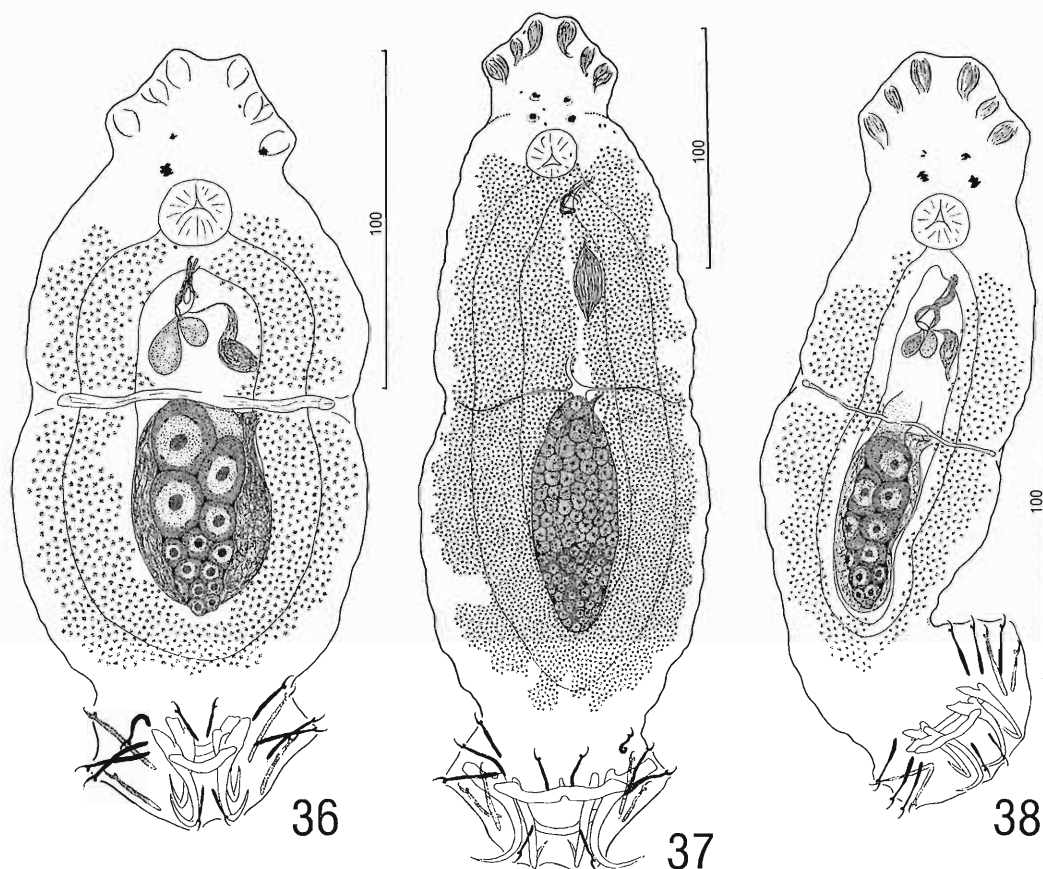
Boeger and Kritsky (1988) found only a few specimens of *Amphithecium catalaoensis* from a single location (among 6) within the Amazon Basin. They suggested that *Pygocentrus nattereri* was not a required host or that the parasite originated from the black waters of the Rio Negro. Lago Tapaná is the lower lake of the Rio Uatumã and is characterized by black water during the annual low-water period of the Amazon Basin. During high-water periods, however, the lake contains a mixture of white and black water as a result of back flooding from the main Amazon. These periodic hydrochemical features of Lago Tapaná are similar to those occurring within the Furo do Catalão where *A. catalaoensis* was originally collected. Because *A. catalaoensis* had a low prevalence and intensity on *P. nattereri* in both the Furo do Catalão and Lago Tapaná during respective studies and has not been collected from habitats characterized by either black or white water, it appears that the parasite may be suited to locations in the Amazon Basin where periodic mixing of water types occurs.

***Amphithecium diclonophallum* sp. n. (Figs. 36, 39–47)**

TYPE HOST AND LOCALITY: *Serrasalmus rhombeus*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

OTHER RECORDS: *Pristobrycon* sp.: Rio Negro near Manaus, Amazonas (28 December 1988). *Serrasalmus compressus*: Rio Solimões

29. Ventral bar. 30. Hook pair 7. 31. Hook pair 5. 32. Hook pair 2. 33. Copulatory complex (ventral view). 34. Dorsal bar. 35. Dorsal anchor. All drawings are to the 25- μ m scale.



Figures 36–38. Whole-mount illustrations of *Amphithecium* spp. (composite, ventral views). 36. *Amphithecium diclonophallum* sp. n. (from *Serrasalmus rhombeus*). 37. *Amphithecium microphallum* sp. n. (from *Pygocentrus nattereri*). 38. *Amphithecium minutum* sp. n. (from *Serrasalmus spilopleura*). All drawings are to respective 100- μ m scales.

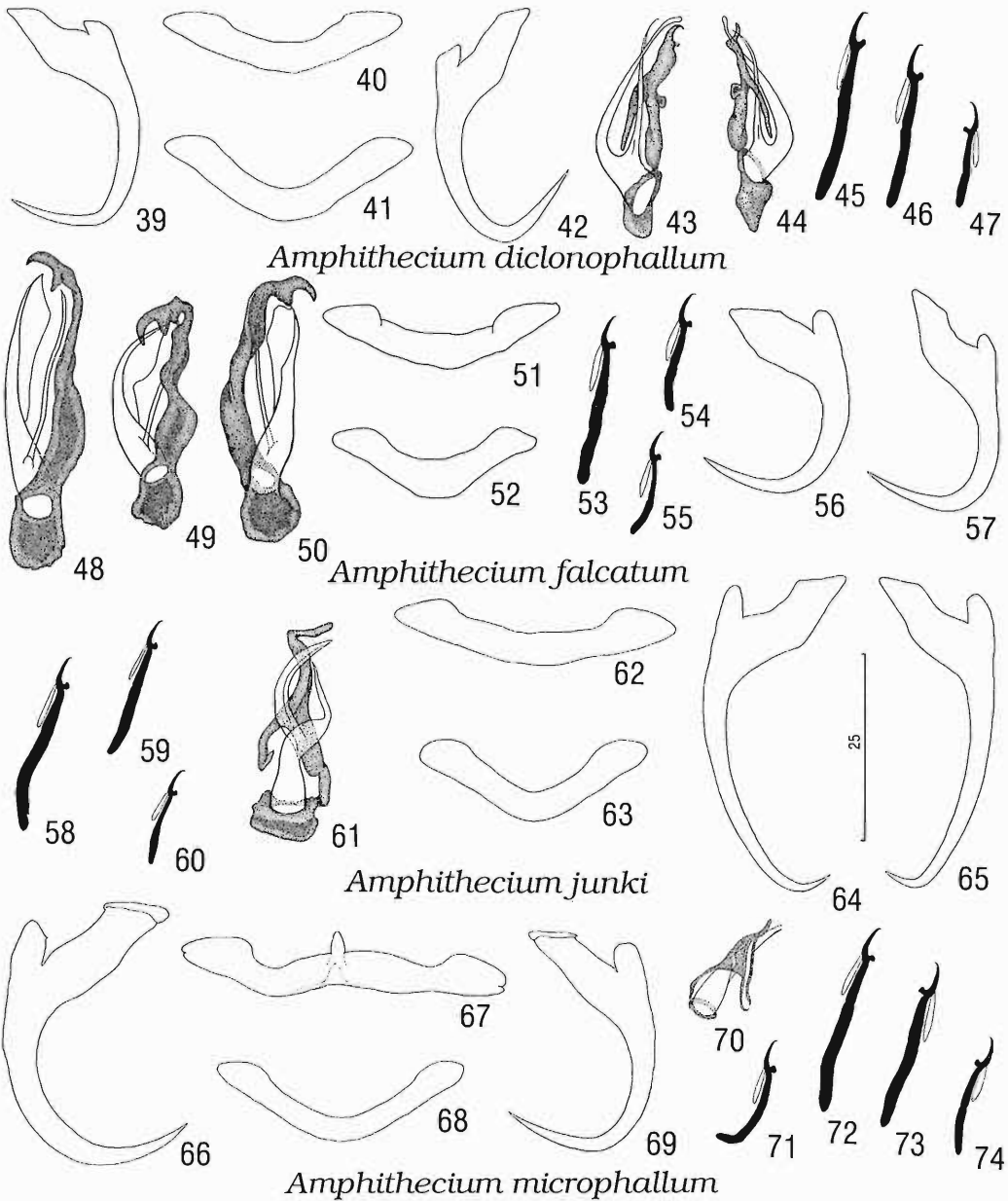
near Ilha da Marchantaria, Manaus, Amazonas (28 October 1993). *Serrasalmus elongatus*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989). *Serrasalmus gouldingi*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989). *Serrasalmus rhombeus*: Rio Uatumã, Amazonas (no date). *Serrasalmus* sp. (2 of Jégu): Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Rio Uatumã, Lago Tapaná, near Santana, Amazonas (3 November 1989); Santa Luzia, Rio Uatumã, Amazonas (20 September 1985).

SPECIMENS STUDIED: Holotype, INPA PLH 241; 11 paratypes, INPA PLH 242, USNPC 85794, 85795, HWML 38592 from *S. rhombeus*. 1 voucher from *Pristobrycon* sp., USNPC 85801; 2 vouchers from *S. compressus*, USNPC 85800; 5 vouchers from *S. elongatus*, USNPC 85799; 9 vouchers from *S. gouldingi*, USNPC

85802; 5 vouchers from *Serrasalmus* sp. (2 of Jégu), USNPC 85796, 85797, 85798.

COMPARATIVE MEASUREMENTS: Table 1.

DESCRIPTION: Body broad, fusiform, slightly constricted near midlength; greatest width near midlength. Tegument smooth. Cephalic lobes moderately developed. Eyes 4, equidistant; posterior pair larger than anterior pair; 1 or both members of each pair infrequently absent; accessory granules uncommon in cephalic, anterior trunk regions. Pharynx spherical. Peduncle broad. Anchors similar; each with well-differentiated roots, evenly curved shaft, elongate point. Bars similar; each broadly V- or U-shaped, with small terminal enlargements. Copulatory organ with 2 subequal rami; primary ramus with small terminal bulb, secondary ramus acute; base with small proximal flap. Articula-



Figures 39–74. Sclerotized structures of *Amphithecium* spp. 39–47. *Amphithecium diclonophallum* sp. n. (from *Serrasalmus rhombeus*). 39. Ventral anchor. 40. Ventral bar. 41. Dorsal bar. 42. Dorsal anchor. 43. Copulatory complex (dorsal view). 44. Copulatory complex (ventral view). 45. Hook pair 7. 46. Hook pair 4. 47. Hook pair 5. 48–57. *Amphithecium falcatum* Boeger and Kritsky, 1968 (from *Serrasalmus spilopleura*). 48, 49. Copulatory complexes (dorsal views). 50. Copulatory complex (ventral view). 51. Ventral bar. 52. Dorsal bar. 53. Hook pair 3. 54. Hook pair 1. 55. Hook pair 5. 56. Ventral anchor. 57. Dorsal anchor. 58–65. *Amphithecium junki* Boeger and Kritsky, 1968 (from *Pygocentrus nattereri*). 58. Hook pair 7. 59. Hook pair 1. 60. Hook pair 5. 61. Copulatory complex (dorsal view). 62. Ventral bar. 63. Dorsal bar. 64. Ventral anchor. 65. Dorsal anchor. 66–74. *Amphithecium microphallum* sp. n. (from *Pygocentrus nattereri*). 66. Ventral anchor. 67. Ventral bar. 68. Dorsal bar. 69. Dorsal anchor. 70. Copulatory complex (ventral view). 71. Hook pair 1. 72. Hook pair 7. 73. Hook pair 3. 74. Hook pair 5. All drawings are to the 25- μ m scale.

Table 1. Comparative measurements (in micrometers) of *Amphithecium diclonophallum* sp. n., from 6 serrasalmid hosts.

	<i>Pristobrycon</i> sp.	<i>N</i>	<i>Serrasalmus</i> <i>compressus</i>	<i>N</i>	<i>Serrasalmus</i> <i>elongatus</i>	<i>N</i>	<i>Serrasalmus</i> <i>gouldingi</i>	<i>N</i>	<i>Serrasalmus</i> <i>rhombeus</i>	<i>N</i>	<i>Serrasalmus</i> sp. (2 of Jégu)	<i>N</i>
Body												
Length	—	—	—	—	—	—	246	1	233 (224–239)	4	—	—
Width	—	—	—	—	—	—	117	1	101 (94–109)	4	—	—
Haptor												
Length	—	—	—	—	—	—	54	1	56 (52–63)	3	—	—
Width	—	—	—	—	—	—	76	1	76 (70–81)	3	—	—
Pharynx												
Diameter	—	—	—	—	—	—	19	1	17 (16–19)	4	—	—
Copulatory organ												
Length	34	1	32 (30–34)	2	34 (33–36)	3	35 (33–38)	7	30 (26–32)	7	30–31	5
Accessory piece												
Length	24	1	20 (18–22)	2	21–22	4	22 (20–23)	7	20 (18–22)	6	18 (16–20)	5
Dorsal anchor												
Length	—	—	33	1	36 (33–38)	5	35 (29–37)	6	33 (32–35)	6	33 (32–35)	5
Base width	—	—	15	1	13 (12–14)	4	14 (11–16)	3	14 (13–15)	4	14 (13–15)	4
Ventral anchor												
Length	32	1	34	2	34 (33–35)	5	33 (31–34)	7	32 (31–34)	8	32 (31–33)	5
Base width	13	1	13 (12–14)	2	14–15	5	13–14	6	13–14	6	15 (14–16)	5
Bar length												
Ventral	—	—	—	—	—	—	34 (33–35)	2	31 (29–32)	3	32	1
Dorsal	—	—	—	—	—	—	31	2	29 (28–30)	3	27	1
Hook lengths												
Pair 1	17	1	17	1	17–18	5	17 (14–19)	7	17–18	4	17 (16–18)	4
Pair 2	21	1	19	1	19–20	5	20 (19–21)	8	20 (19–21)	4	19 (18–20)	4
Pair 3	25	1	23	1	23–24	5	23 (22–25)	7	22 (21–23)	8	23 (22–25)	5
Pair 4	—	—	26	1	26–27	5	26 (23–28)	5	26 (25–28)	8	27 (25–29)	4
Pair 5	—	—	15	1	15–16	4	15–16	5	15–16	5	16–17	3
Pair 6	—	—	21	2	19–20	5	19 (16–20)	5	20 (19–21)	5	19–20	3
Pair 7	—	—	25 (24–26)	2	26–27	4	26 (20–29)	6	26 (25–28)	6	26 (24–27)	4
Germarium												
Length	—	—	—	—	—	—	47	1	48 (41–61)	4	—	—
Width	—	—	—	—	—	—	36	1	27 (24–31)	4	—	—
Testis												
Length	—	—	—	—	—	—	55	1	52 (48–60)	3	—	—
Width	—	—	—	—	—	—	31	1	28 (24–31)	3	—	—

tion process of accessory piece with short sub-terminal flap, distal rod robust with hooked end. Testis ovate. Germarium conical; oviduct, ootype, uterus not observed; vitellaria dense throughout trunk, absent in regions of reproductive organs.

REMARKS: This species resembles *Amphithecium speirocamarotum* sp. n. in the comparative morphology of the accessory piece. *Amphithecium diclonophallum* is distinct in possessing anchors with short shafts, a bulbous termination

of the primary ramus of the copulatory organ, and an elongate acute secondary ramus of the copulatory organ. The specific name is from Greek (*di* ["two"]) + *klon* ["branch"] + *phallos* ["penis"]) and refers to the copulatory organ.

***Amphithecium falcatum* Boeger and Kritsky, 1988 (Figs. 48–57)**

RECORDS: *Pristobrycon* sp.: Rio Negro near Manaus, Amazonas (28 December 1988). *Pygocentrus nattereri*: Rio Uatumã, Lago Tapaná,

near Santana, Amazonas (3 November 1989); Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas (26 November 1984). *Serrasalmus compressus*: Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas (27, 28 October 1993). *Serrasalmus elongatus*: Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas (26 November 1984). *Serrasalmus gouldingi*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989). *Serrasalmus manuellii*: Kaikuta, Rio Xingu, Pará (10 October 1992). *Serrasalmus rhombeus*: Rio Capucapú at its confluence with Rio Jatapú, Cachoeira das Garças, Amazonas (31 October 1989); Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Rio Uatumã, Lago Tapaná, Santana, Amazonas (3 November 1989). *Serrasalmus spilopleura*: Rio Uatumã, Lago Tapaná, near Santana, Amazonas (3 November 1989). *Serrasalmus* sp. (2 of Jégu): Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Rio Uatumã, Lago Tapaná, Santana, Amazonas (3 November 1989). *Serrasalmus* sp. (2n = 58): Furo do Catalão, near Manaus, Amazonas (5 January 1989); Ilha do Carreiro, near Manaus, Amazonas.

PREVIOUS RECORDS: *Pygocentrus nattereri* (type host): Furo do Catalão, Manaus, Amazonas (type locality); Ilha da Marchantaria, Rio Solimões, Manaus, Amazonas; Rio Pacaás-Novos, Guajará-Mirim, Rondônia; Rio Mamoré, Surpresa, Rondônia; Rio Guaporé, Surpresa, Rondônia; Rio Guaporé, Costa Marques, Rondônia (all Boeger and Kritsky, 1988).

SPECIMENS STUDIED: Two vouchers from *Pristobrycon* sp., USNPC 85812; 16 vouchers from *Pygocentrus nattereri*, USNPC 85808, 85809; 12 vouchers from *Serrasalmus compressus*, USNPC 85815; 15 vouchers from *S. elongatus*, USNPC 85807; 37 vouchers from *S. gouldingi*, USNPC 85811; 3 vouchers from *S. manuellii*, USNPC 85810; 28 vouchers from *S. rhombeus*, USNPC 85804, 85805, 85806; 21 vouchers from *S. spilopleura*, USNPC 85803; 14 vouchers from *Serrasalmus* sp. (2 of Jégu), USNPC 85816, 85817; 50 vouchers from *Serrasalmus* sp. (2n = 58), USNPC 85813, 85814.

COMPARATIVE MEASUREMENTS: Table 2.

REMARKS: *Amphithecium falcatum* is known from 10 species of *Pygocentrus*, *Pristobrycon*, and *Serrasalmus*. Specimens from respective hosts showed minimal variation in morphology and size. *Amphithecium falcatum* resembles *A. unguiculum* in having the distal rod of the ac-

cessory piece incorporated into the proximal articulation process. However, *A. falcatum* has a terminal hook of the distal rod of the accessory piece, whereas that of *A. unguiculum* is C-shaped.

Amphithecium junki Boeger and Kritsky, 1988 (Figs. 58–65)

RECORDS: *Pygocentrus nattereri*: Rio Uatumã, Lago Tapaná, near Santana, Amazonas (3 November 1989); Furo do Catalão, Manaus, Amazonas (26, 27 November 1984); Ilha da Marchantaria, Rio Solimões, Manaus, Amazonas (25 November 1984). *Serrasalmus rhombeus*: Ilha da Marchantaria, Rio Solimões, Manaus, Amazonas (26 November 1984).

PREVIOUS RECORDS: *Pygocentrus nattereri* (type host): Furo do Catalão, Manaus, Amazonas (type locality); Ilha da Marchantaria, Rio Solimões, Manaus, Amazonas; Rio Pacaás-Novos, Guajará-Mirim, Rondônia; Rio Mamoré, Surpresa, Rondônia; Rio Guaporé, Surpresa, Rondônia; Rio Guaporé, Costa Marques, Rondônia (all Boeger and Kritsky, 1988).

SPECIMENS STUDIED: Twenty-one vouchers from *P. nattereri*, USNPC 85819, 85820, 85821; 1 voucher from *S. rhombeus*, USNPC 85818.

COMPARATIVE MEASUREMENTS (dimensions of the specimen from *S. rhombeus* follow those of *P. nattereri* in brackets): Body length 280 ($n = 1$), greatest width 112 ($n = 1$); haptor length 66 ($n = 1$), width 85 ($n = 1$); pharyngeal diameter 15 ($n = 1$); ventral anchor length 43 (40–45; $n = 17$) [41 (40–43; $n = 2$)], base width 16 (15–17; $n = 12$) [17 ($n = 2$)]; dorsal anchor length 43 (39–45; $n = 11$) [41 (40–42; $n = 2$)], base width 16 (13–17; $n = 7$) [15 (14–16; $n = 2$)]; ventral bar 34 ($n = 1$), dorsal bar 32 ($n = 1$) long; hook pairs 1, 2, 6–21 (17–23; $n = 39$) [20–21 ($n = 2$)], pairs 3, 4, 7–26 (22–28; $n = 43$) [26–27 ($n = 5$)], pair 5–14–15 ($n = 11$) [15 (14–16; $n = 2$)] long; copulatory organ length 27 (24–29; $n = 14$) [28 ($n = 1$)], accessory piece length 22 (20–27; $n = 10$) [24 ($n = 1$)]; testis 64 ($n = 1$) long, 28 ($n = 1$) wide; germarium 66 ($n = 1$) long, 25 ($n = 1$) wide.

REMARKS: *Amphithecium junki* normally occurs on *Pygocentrus nattereri*. The specimen from *Serrasalmus rhombeus* is probably accidental.

Table 2. Comparative measurements (in micrometers) of *Amphithecium falcatum* Boeger and Kritsky, 1988, from 10 serrasalmid hosts.

	<i>Pristobrycon</i> sp.	N	<i>Pygocentrus</i> <i>nattereri</i>	N	<i>Serrasalmus</i> <i>compressus</i>	N	<i>Serrasalmus</i> <i>elongatus</i>	N	<i>Serrasalmus</i> <i>gouldingi</i>	N
Body										
Length	—	—	249 (222–275)	2	—	—	249 (217–285)	3	325 (257–373)	17
Width	—	—	113 (111–115)	2	—	—	78 (64–86)	3	121 (96–152)	19
Haptor										
Length	—	—	45–46	2	—	—	54 (50–59)	3	65 (55–78)	18
Width	—	—	67 (66–69)	2	—	—	74 (72–79)	3	92 (78–107)	18
Pharynx										
Diameter	—	—	18	2	—	—	16 (14–17)	3	21 (18–23)	19
Copulatory organ										
Length	44	1	40 (38–48)	12	37 (35–39)	3	39 (38–41)	6	43 (40–48)	12
Accessory piece										
Length	34	1	32 (28–41)	12	30 (27–32)	3	33 (31–36)	5	36 (34–39)	12
Dorsal anchor										
Length	36 (35–37)	2	31 (28–36)	14	31 (30–32)	3	31 (29–34)	9	37 (33–40)	12
Base width	14 (12–16)	2	14 (12–16)	9	14	2	13 (12–14)	8	15 (13–16)	9
Ventral anchor										
Length	31	2	28 (24–31)	15	27 (26–28)	4	27 (24–28)	10	31 (28–34)	15
Base width	18 (16–19)	2	15 (14–16)	14	15	2	14–15	10	16 (14–19)	11
Bar length										
Ventral	—	—	26	1	—	—	28 (26–30)	3	30 (27–34)	11
Dorsal	—	—	22	1	—	—	25 (23–26)	3	28 (24–34)	13
Hook lengths										
Pair 1	17	1	17 (16–18)	8	16	3	16–17	8	18 (16–19)	8
Pair 2	—	—	20 (18–22)	10	21 (20–22)	2	21 (19–22)	7	22 (21–25)	7
Pair 3	24	1	24 (23–26)	12	24 (22–25)	3	24 (23–25)	9	26 (25–28)	11
Pair 4	26	1	25 (24–27)	11	25 (23–27)	3	25 (24–26)	6	27 (25–28)	12
Pair 5	—	—	14–15	10	14	2	14–15	4	15 (14–16)	6
Pair 6	—	—	18 (16–19)	10	18	2	18 (17–19)	8	19 (18–21)	12
Pair 7	27	1	23 (21–25)	9	21–22	3	22 (21–24)	4	26 (24–27)	10
Germarium										
Length	—	—	59 (57–60)	2	—	—	53 (41–72)	3	66 (51–88)	18
Width	—	—	31 (28–33)	2	—	—	23 (18–27)	3	32 (28–35)	18
Testis										
Length	—	—	66 (56–75)	2	—	—	47 (41–55)	3	68 (54–88)	14
Width	—	—	37 (35–39)	2	—	—	23 (16–31)	3	34 (26–45)	14

***Amphithecium microphallum* sp. n.**
(Figs. 37, 66–74)

TYPE HOST AND LOCALITY: *Pygocentrus nattereri*: Rio Uatumã, Lago Tapaná, near Santana, Amazonas (3 November 1989).

OTHER RECORD: *Serrasalmus* sp. (2n = 58): Furo do Catalão, Manaus, Amazonas (30 January 1991).

SPECIMENS STUDIED: Holotype, INPA PLH 236; 17 paratypes, INPA PLH 237, USNPC 85822, HWML 38593 from *Pygocentrus natter-*

eri; 2 vouchers from *Serrasalmus* sp. (2n = 58), USNPC 85823.

COMPARATIVE MEASUREMENTS: Measurements of specimens from *Serrasalmus* sp. (2n = 58) are in brackets following those of the type series.

DESCRIPTION: Body 343 (289–401; n = 9) long, robust, fusiform, slightly flattened dorso-ventrally, with inconspicuous constriction near midlength; greatest width 122 (94–146; n = 9) usually in posterior trunk. Tegument smooth.

Table 2. Extended.

<i>Serrasalmus manuelli</i>	<i>N</i>	<i>Serrasalmus rhombeus</i>	<i>N</i>	<i>Serrasalmus spilopleura</i>	<i>N</i>	<i>Serrasalmus</i> sp. (2 of Jégu)	<i>N</i>	<i>Serrasalmus</i> sp. (2n = 58)	<i>N</i>
—	—	266 (208–345)	6	253 (219–294)	7	—	—	215 (190–261)	9
—	—	103 (88–110)	5	94 (79–108)	8	—	—	87 (61–102)	9
—	—	53 (41–61)	6	52 (43–62)	7	—	—	48 (42–57)	7
—	—	82 (75–96)	5	80 (71–95)	6	—	—	73 (70–78)	6
—	—	18 (17–19)	6	18 (16–20)	8	—	—	18 (15–24)	9
43	2	42 (38–45)	16	34 (29–42)	9	40 (35–43)	11	40 (35–44)	19
32 (30–35)	2	34 (31–37)	12	29 (26–32)	6	32 (29–35)	10	32 (27–37)	17
35 (32–36)	3	34 (28–36)	14	31 (28–33)	12	33 (29–37)	11	32 (29–36)	26
14–15	2	15 (13–16)	8	13 (12–14)	9	14 (10–16)	7	14 (11–15)	14
29	3	29 (24–31)	13	27 (25–29)	13	28 (26–30)	12	28 (25–30)	27
15 (14–16)	3	16 (15–17)	11	14–15	12	16 (15–18)	12	15 (14–16)	23
—	—	29 (28–30)	3	28 (26–29)	5	—	—	29 (25–38)	7
—	—	24 (22–28)	5	24 (22–26)	6	—	—	26 (19–33)	6
16	1	17 (16–18)	8	16 (15–17)	11	16–17	5	17 (16–18)	17
21–22	3	21 (20–22)	7	22 (20–23)	9	21 (20–22)	9	21 (18–25)	19
26–27	2	26 (24–28)	10	24 (23–26)	12	24–25	7	26 (23–29)	21
26 (25–28)	3	27 (25–28)	8	26 (25–27)	9	26 (24–27)	8	26 (25–29)	27
14	1	14–15	4	14 (13–15)	8	15 (14–16)	6	15 (14–16)	16
19 (18–21)	3	19 (18–21)	13	18 (17–19)	6	18 (17–20)	7	19 (17–20)	17
25 (24–27)	3	25 (24–26)	11	23 (22–24)	9	24 (22–25)	8	23 (21–27)	18
—	—	51 (39–66)	6	46 (35–60)	6	—	—	42 (31–58)	9
—	—	24 (20–29)	6	29 (22–32)	6	—	—	24 (18–28)	9
—	—	50 (39–62)	5	59 (46–68)	5	—	—	45 (35–55)	5
—	—	26 (18–31)	5	30 (25–35)	5	—	—	27 (20–31)	5

Cephalic region narrow in comparison to trunk, directed anteromedially from trunk; lobes moderately developed. Eyes 4, equidistant; posterior members larger; accessory granules usually numerous in cephalic, anterior trunk regions. Pharynx spherical, 21 (19–24; $n = 9$) in diameter. Peduncle broad; haptor 64 (52–73; $n = 9$) long, 92 (80–99; $n = 9$) wide. Anchors similar; each with elongate slightly depressed superficial root, prominent deep root, curved shaft, elongate point; shaft, point of ventral anchor forming even arc; ventral anchor 37 (35–40; $n = 9$) [36–

37 ($n = 4$)] long, base 21 (18–22; $n = 8$) [21–22 ($n = 4$)] wide; dorsal anchor 32 (31–33; $n = 8$) [33 (32–34; $n = 3$)] long, base 16 (14–17; $n = 6$) [18 ($n = 1$)] wide. Ventral bar 42 (38–44; $n = 8$) long, wavy or straight, with enlarged terminations, short anteromedial projection, posterodorsal V-shaped indentation. Dorsal bar 34 (33–36; $n = 7$) long, broadly U-shaped, with small terminal enlargements. Hook pairs 1, 5–18 (16–20; $n = 8$) [16–17 ($n = 4$)], pairs 2, 3, 6–22 (21–24; $n = 22$) [23 (22–25; $n = 6$)], pairs 4, 7–26 (23–28; $n = 17$) [26 (24–28; n

= 6)] long. Copulatory organ 17 (16–18; $n = 4$) [16–17 ($n = 2$)] long, delicate, tubular, tapered; base lacking proximal flap. Accessory piece 13 (12–15; $n = 5$) [13–14 ($n = 2$)] long, with double distal rod blunt terminally. Gonads elongate ovate; testis 56 (47–61; $n = 3$) long, 24–25 ($n = 3$) wide; prostatic reservoirs not observed. Germarium 77 (57–92; $n = 8$) long, 29 (26–32) wide; oviduct, ootype not observed; vaginae with delicate narrow lateral canals, vaginal apertures uncertain. Vitellaria dense throughout trunk except absent along midline.

REMARKS: *Amphithecium microphallum* is unique in having an anteromedial process and a posterodorsal indentation on the ventral bar. The specific name is from Greek (*mikros* ["small"]) + *phallos* ["penis"]) and refers to the comparatively small copulatory complex.

***Amphithecium minutum* sp. n.**

(Figs. 38, 78–85)

TYPE HOST AND LOCALITY: *Serrasalmus spilopleura*: Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas (14 September 1984).

OTHER RECORDS: *Pristobrycon eigenmanni*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Nazaré, Rio Uatumã, Amazonas (17 September 1985); Santa Luzia, Rio Uatumã, Amazonas (20 September 1985); Rio Negro near Manaus, Amazonas (28 December 1988). *Pristobrycon* sp.: Rio Negro near Manaus, Amazonas (28 December 1988). *Serrasalmus gouldingi*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989). *Serrasalmus spilopleura*: Rio Uatumã, Lago Tapaná, near Santana, Amazonas (3 November 1989).

SPECIMENS STUDIED: Holotype, INPA PLH 246; 17 paratypes, INPA PLH 247, USNPC 85824, 85825, HWML 38594 from *S. spilopleura*; 27 vouchers from *P. eigenmanni*, USNPC 85826, 85827, 85828, 85829; 3 vouchers from *Pristobrycon* sp., USNPC 85830; 12 vouchers from *S. gouldingi*, USNPC 85831.

COMPARATIVE MEASUREMENTS: Table 3.

DESCRIPTION: Body fusiform, constricted near midlength; greatest width in anterior or posterior trunk. Tegument smooth or with scaled annulations. Cephalic lobes moderately developed. Eyes 4, equidistant; posterior pair larger than anterior pair; 1 or both members of anterior pair frequently absent; accessory granules uncommon in cephalic, anterior trunk regions. Pharynx spherical. Peduncle broad. Anchors

similar; each with well-developed roots, evenly curved shaft, elongate point. Bars similar; each broadly V- or U-shaped, with small terminal enlargements. Copulatory organ tapered, conical, frequently sigmoid; base with prominent proximal flap. Articulation process of accessory piece bowed; distal rod uniting with base of copulatory organ, distally variable, blunt. Testis subovate. Germarium conical; oviduct short; ootype, uterus not observed; vaginae slightly expanded immediately proximal to vaginal openings. Vitellaria dense throughout trunk, absent in regions of reproductive organs.

REMARKS: *Amphithecium minutum* differs from congeneric species by having both the articulation process and distal rod of the accessory piece articulating to the base of the copulatory organ. The specific name is from Latin (*minuta* ["small"]) and refers to the small size of this helminth.

***Amphithecium muricatum* sp. n.**

(Figs. 75, 86–94)

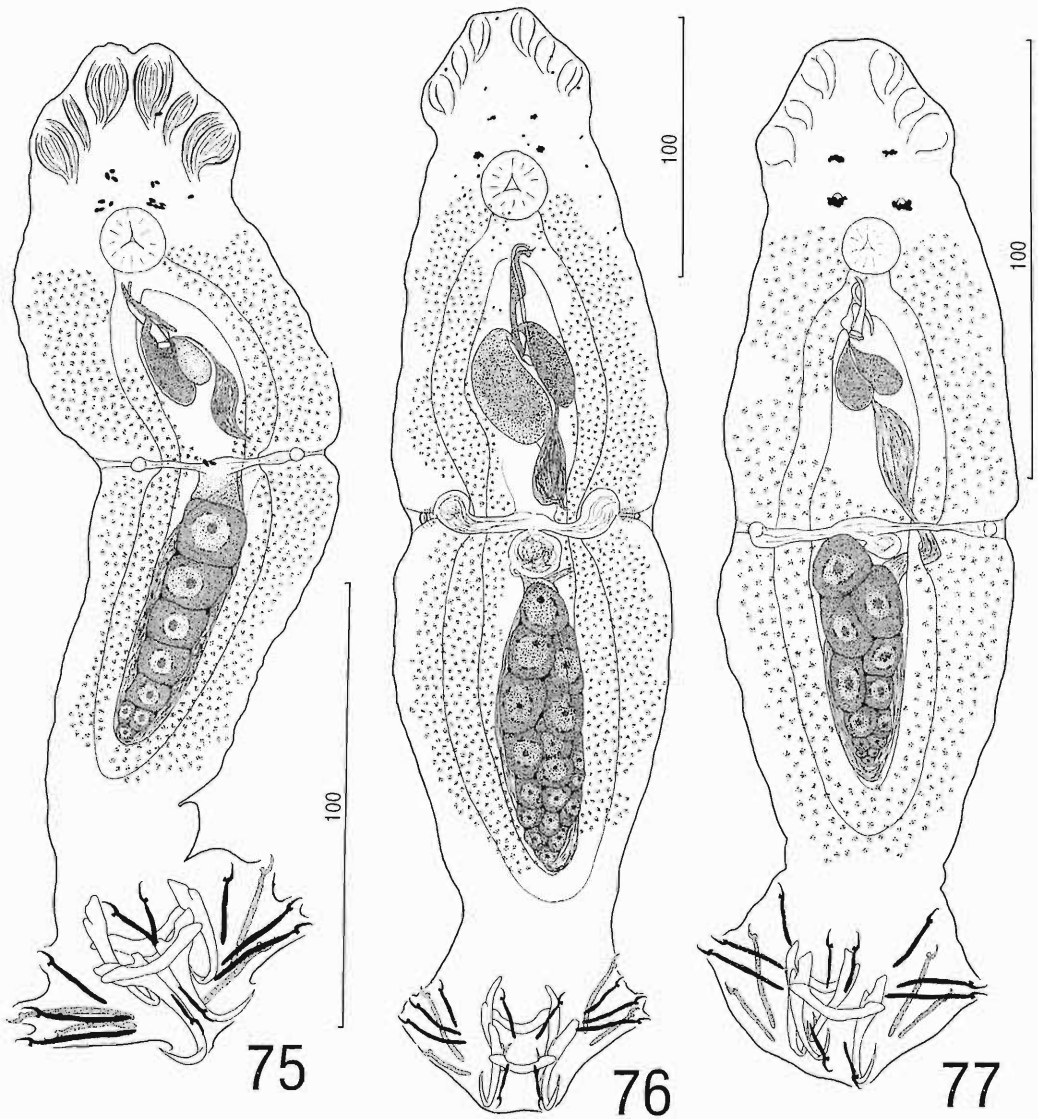
TYPE HOST AND LOCALITY: *Pristobrycon eigenmanni*: Nazaré, Rio Uatumã, Amazonas (17 September 1985).

OTHER RECORDS: *Pristobrycon eigenmanni*: Santa Luzia, Rio Uatumã, Amazonas (20 September 1985). *Serrasalmus rhombeus*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Rio Pitinga, Igarapé Água Branca, Rio Uatumã, Amazonas (15 September 1985). *Serrasalmus* sp. (2 of Jégu): Nazaré, Rio Uatumã, Amazonas (17 September 1985).

SPECIMENS STUDIED: Holotype, INPA PLH 238; 18 paratypes, INPA PLH 239, PLH 240, USNPC 85832, 85833, HWML 38595 from *Pristobrycon eigenmanni*; 16 vouchers from *Serrasalmus rhombeus*, USNPC 85835, 85836; 1 voucher from *Serrasalmus* sp. (2 of Jégu), USNPC 85834.

COMPARATIVE MEASUREMENTS: Table 4.

DESCRIPTION: Body fusiform; trunk constricted near midlength, tapered posteriorly; greatest width usually in anterior trunk. Tegument smooth or with scaled annulations. Cephalic lobes moderately developed. Eyes 4, equidistant, comprised of few loosely associated granules; posterior members larger, farther apart than anterior pair; accessory granules in cephalic, anterior trunk regions. Pharynx spherical. Peduncle moderate to narrow. Anchors similar; each with well-differentiated slightly depressed

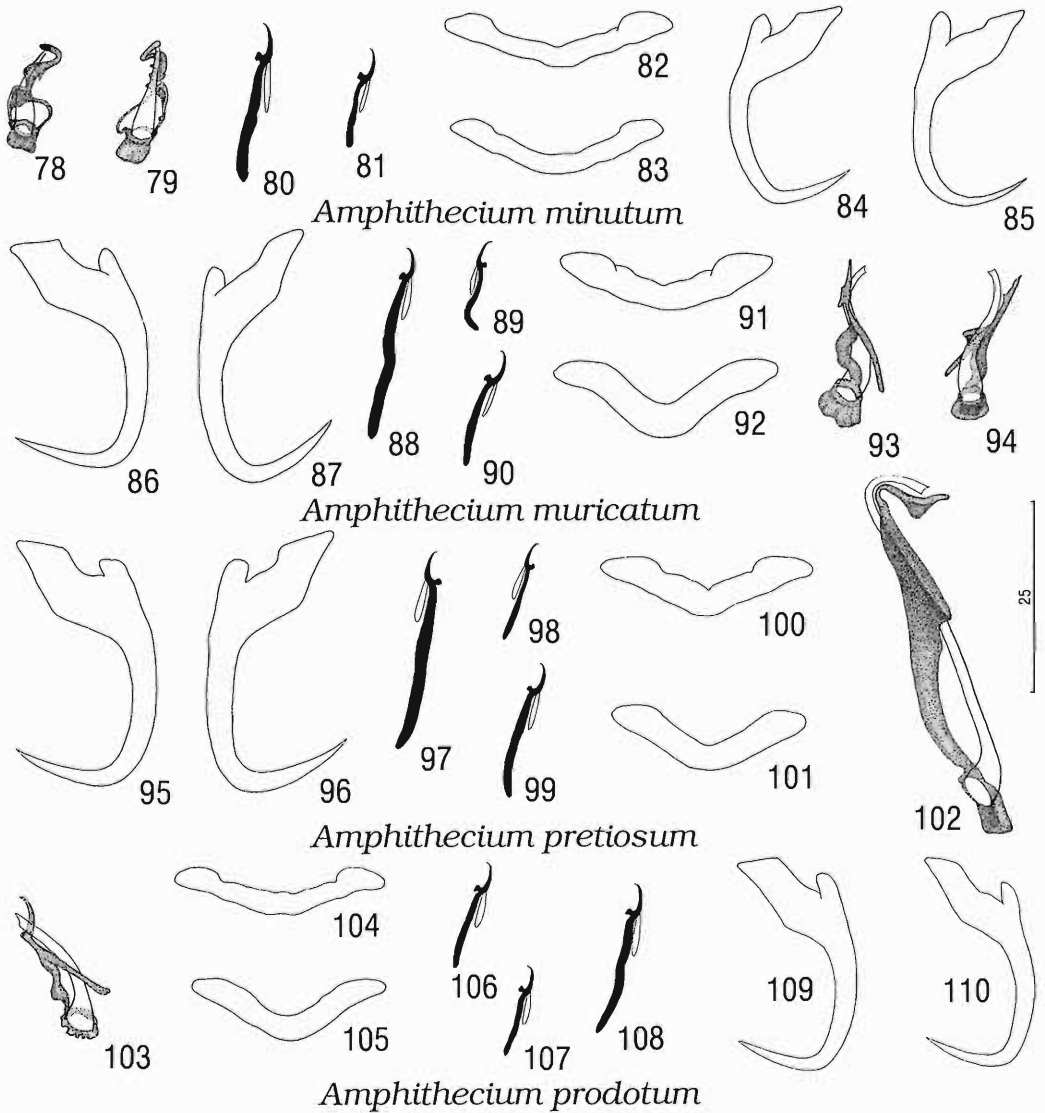


Figures 75–77. Whole-mount illustrations of *Amphithecium* spp. (composite, ventral views). 75. *Amphithecium muricatum* sp. n. (from *Pristobrycon eigenmanni*). 76. *Amphithecium pretiosum* sp. n. (from *Serrasalmus gouldingi*). 77. *Amphithecium prodotum* sp. n. (from *Pristobrycon striolatus*). All drawings are to respective 100- μ m scales.

superficial root, short deep root, gently curved shaft, elongate point. Ventral bar broadly V-shaped, with enlarged terminations; dorsal bar bent at midlength, with ends directed laterally. Copulatory organ sigmoid, tapered; base with short proximal flap. Distal rod of accessory piece straight, terminally pointed, with subterminal expansion. Testis elongate ovate; prostatic reservoirs large. Germarium conical; oviduct short;

ootype, uterus not observed. Vitellaria throughout trunk except absent in regions of reproductive organs.

REMARKS: The haptor armaments of *Amphithecium muricatum*, *A. minutum*, and *A. prodotum* are similar. *Amphithecium muricatum* differs from *A. minutum* by having a free proximal end of the distal rod of the accessory piece (articulated with base of copulatory organ in *A.*



Figures 78–110. Sclerotized structures of *Amphithecium* spp. 78–85. *Amphithecium minutum* sp. n. (from *Serrasalmus spilopleura*). 78. Copulatory complex (ventral view). 79. Copulatory complex (dorsal view). 80. Hook pair 7. 81. Hook pair 1. 82. Ventral bar. 83. Dorsal bar. 84. Ventral anchor. 85. Dorsal anchor. 86–94. *Amphithecium muricatum* sp. n. (from *Pristobrycon eigenmanni*). 86. Ventral anchor. 87. Dorsal anchor. 88. Hook pair 7. 89. Hook pair 5. 90. Hook pair 1. 91. Ventral bar. 92. Dorsal bar. 93. Copulatory complex (ventral view). 94. Copulatory complex (dorsal view). 95–102. *Amphithecium pretiosum* sp. n. (from *Serrasalmus gouldingi*). 95. Ventral anchor. 96. Dorsal anchor. 97. Hook pair 7. 98. Hook pair 5. 99. Hook pair 2. 100. Ventral bar. 101. Dorsal bar. 102. Copulatory complex (ventral view). 103–110. *Amphithecium prodotum* sp. n. (from *Pristobrycon striolatus*). 103. Copulatory complex (ventral view). 104. Ventral bar. 105. Dorsal bar. 106. Hook pair 1. 107. Hook pair 5. 108. Hook pair 7. 109. Ventral anchor. 110. Dorsal anchor. All drawings are to the 25- μ m scale.

Table 3. Comparative measurements (in micrometers) of *Amphithecium minutum* sp. n., from 4 serrasalmid hosts.

	<i>Pristobrycon eigenmanni</i>	<i>N</i>	<i>Pristobrycon sp.</i>	<i>N</i>	<i>Serrasalmus gouldingi</i>	<i>N</i>	<i>Serrasalmus spilopleura</i>	<i>N</i>
Body								
Length	209 (170–245)	11	—	—	305 (273–329)	6	226 (195–271)	9
Width	58 (45–72)	14	—	—	87 (73–96)	6	74 (61–92)	9
Haptor								
Length	51 (46–59)	13	—	—	63 (55–78)	5	49 (44–59)	9
Width	60 (45–67)	13	—	—	83 (71–107)	5	65 (57–74)	9
Pharynx								
Diameter	13 (11–15)	13	—	—	16–17	6	15 (14–16)	9
Copulatory organ								
Length	18 (16–20)	8	19–20	2	19 (18–21)	6	19 (15–20)	6
Accessory piece								
Length	16 (14–17)	8	16–17	3	17 (16–18)	6	15 (12–17)	6
Dorsal anchor								
Length	31 (28–32)	9	30 (29–31)	3	31 (30–32)	5	27 (25–29)	8
Base width	12 (11–14)	9	12–13	3	11 (10–13)	3	11 (9–13)	7
Ventral anchor								
Length	32 (28–34)	12	30 (29–31)	3	30 (29–31)	5	26 (23–27)	8
Base width	12 (11–13)	12	12–13	3	12–13	5	11 (10–12)	8
Bar length								
Ventral	28 (26–30)	11	—	—	30–31	6	29 (26–30)	5
Dorsal	27 (24–28)	11	—	—	28 (25–29)	6	27 (24–29)	5
Hook lengths								
Pair 1	14 (13–15)	6	13	1	13–14	3	12–13	5
Pair 2	19 (17–20)	10	19 (18–20)	2	20 (19–21)	3	19–20	6
Pair 3	22 (20–23)	11	22–23	3	22–23	3	21 (20–22)	7
Pair 4	24 (21–25)	10	23 (22–24)	3	22 (21–23)	4	22 (21–23)	7
Pair 5	13 (12–14)	9	13 (12–14)	2	13	4	12–13	5
Pair 6	17 (16–18)	10	17–18	3	16–17	4	15–16	8
Pair 7	24 (22–26)	9	25 (23–26)	3	25 (24–26)	5	23 (22–25)	8
Germarium								
Length	38 (34–42)	6	—	—	48 (32–59)	6	44 (41–46)	4
Width	12 (10–13)	5	—	—	21 (17–23)	5	19–20	4
Testis								
Length	35 (31–42)	3	—	—	59 (51–71)	4	48 (47–49)	3
Width	13 (12–15)	3	—	—	23 (20–26)	3	20 (16–22)	3

minutum) and by lacking enlarged ends on the dorsal bar. The distal rod of the accessory piece of *A. prodotum* has an indistinct distal hook (rod lacking hook in *A. muricatum*). The specific name is from Latin (*muricatus* [“pointed”]) and refers to the copulatory organ.

***Amphithecium pretiosum* sp. n.**
(Figs. 76, 95–102)

TYPE HOST AND LOCALITY: *Serrasalmus gouldingi*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

OTHER RECORDS: *Pristobrycon* sp.: Rio Negro near Manaus, Amazonas (28 December 1988). *Serrasalmus gouldingi*: Rio Uatumã, C. Miriti, Amazonas (26 September 1985). *Serrasalmus manuelli*: Kaikuta, Rio Xingu, Pará (10 October 1992).

SPECIMENS STUDIED: Holotype, INPA PLH 243; 45 paratypes, INPA PLH 244, PLH 245, USNPC 85838, 85839, HWML 38596 from *S. gouldingi*; 2 vouchers from *Pristobrycon* sp., USNPC 85840; 50 vouchers from *S. manuelli*, USNPC 85837.

Table 4. Comparative measurements (in micrometers) of *Amphithecium muricatum* sp. n., from 3 serrasalmid hosts.

	<i>Pristobrycon eigenmanni</i>	<i>N</i>	<i>Serrasalmus rhombeus</i>	<i>N</i>	<i>Serrasalmus</i> sp. (2 of Jégu)	<i>N</i>
Body						
Length	219 (185–288)	6	241 (217–264)	9	—	—
Width	57 (49–62)	7	92 (69–115)	9	—	—
Haptor						
Length	58 (51–66)	6	55 (49–61)	9	—	—
Width	58 (48–69)	6	77 (75–85)	8	—	—
Pharynx						
Diameter	12 (10–14)	7	16 (15–19)	9	—	—
Copulatory organ						
Length	21 (19–24)	8	18 (16–19)	6	21	1
Accessory piece						
Length	17 (16–19)	9	15 (14–16)	6	17	1
Dorsal anchor						
Length	34 (32–36)	7	35 (33–38)	6	32	1
Base width	12 (11–13)	6	13 (12–14)	6	13	1
Ventral anchor						
Length	32 (30–33)	7	33 (31–35)	5	30–31	2
Base width	13 (12–15)	7	14 (13–15)	5	13	2
Bar length						
Ventral	24–25	3	31 (29–33)	6	—	—
Dorsal	23–24	3	30 (27–33)	7	—	—
Hook lengths						
Pair 1	17 (16–18)	9	17 (16–18)	5	17	1
Pair 2	19 (18–21)	6	19–20	4	—	—
Pair 3	23 (21–24)	6	22 (21–23)	5	26	1
Pair 4	25 (21–27)	6	25 (23–27)	5	25	1
Pair 5	14	5	14–15	3	15	1
Pair 6	18 (16–19)	6	17 (16–19)	6	19	1
Pair 7	28 (26–29)	7	26 (25–28)	4	29	1
Germarium						
Length	41 (30–54)	5	52 (38–65)	9	—	—
Width	12 (11–13)	5	23 (13–31)	9	—	—
Testis						
Length	42 (32–47)	4	57 (48–65)	7	—	—
Width	11 (10–13)	4	26 (18–31)	7	—	—

COMPARATIVE MEASUREMENTS: Table 5.

DESCRIPTION: Body fusiform, with constriction at midlength; greatest width usually in anterior trunk. Tegument smooth or with scaled annulations. Cephalic lobes moderately developed. Eyes 4; posterior members larger, farther apart than anterior pair; accessory granules in cephalic, anterior trunk regions. Pharynx spherical. Peduncle broad. Anchors similar; each with well-differentiated depressed roots, straight to slightly arcuate shaft, elongate point. Ventral bar broadly V-shaped,

with enlarged terminations; dorsal bar broadly U-shaped, with slightly enlarged ends. Copulatory organ frequently recurved distally; base with short proximal flap. Articulation process of accessory piece elongate; distal rod with small subterminal keel, blunt. Gonads elongate ovate. Vaginae encircled subterminally by muscle fibers; seminal receptacle a spherical expansion of posterior wall of vaginae, with short connecting duct arising from postero-dextral wall to anterior germarial duct (oviduct); vitellaria throughout trunk except ab-

Table 5. Comparative measurements (in micrometers) of *Amphithecium pretiosum* sp. n., from 3 serrasalmid hosts.

	<i>Pristobrycon</i> sp.	<i>N</i>	<i>Serrasalmus</i> <i>gouldingi</i>	<i>N</i>	<i>Serrasalmus</i> <i>manuelli</i>	<i>N</i>
Body						
Length	—	—	352 (298–428)	20	237	1
Width	—	—	106 (92–132)	19	85	1
Haptor						
Length	—	—	64 (51–79)	18	68	1
Width	—	—	88 (71–99)	20	70	1
Pharynx						
Diameter	—	—	19 (18–23)	20	14	1
Copulatory organ						
Length	55–56	2	55 (48–66)	22	64 (54–78)	35
Accessory piece						
Length	47–48	2	46 (41–58)	23	55 (45–66)	33
Dorsal anchor						
Length	33	1	36 (34–38)	17	38 (36–40)	17
Base width	13	1	14 (13–16)	13	16 (15–18)	13
Ventral anchor						
Length	32	1	34 (32–36)	22	35 (33–37)	20
Base width	12	1	14 (13–17)	20	15 (14–18)	19
Bar length						
Ventral	—	—	29 (28–31)	16	—	—
Dorsal	—	—	27 (25–29)	15	—	—
Hook lengths						
Pair 1	16	1	18 (17–19)	12	18 (17–19)	7
Pair 2	19	1	19 (18–21)	13	19 (18–20)	10
Pair 3	23	1	24 (23–25)	17	24 (22–26)	8
Pair 4	23	1	27 (26–28)	17	27 (25–29)	12
Pair 5	—	—	15 (14–16)	14	15 (14–16)	11
Pair 6	18	1	19 (18–21)	18	20 (19–21)	7
Pair 7	26	1	28 (26–30)	19	29 (28–31)	7
Germaurium						
Length	—	—	65 (40–84)	17	42	1
Width	—	—	26 (19–35)	17	17	1
Egg						
Length	—	—	44 (42–47)	2	—	—
Width	—	—	33 (30–35)	2	—	—
Testis						
Length	—	—	69 (45–77)	11	41	1
Width	—	—	31 (23–39)	11	21	1

sent in regions of reproductive organs. Egg subovate, with short proximal filament.

REMARKS: *Amphithecium pretiosum* possesses circular muscle fibers around the vaginal ducts and a small subterminal keel on the distal rod of the accessory piece, which differentiate it from all other congeneric species. The specific name is from Latin (*pretiosus* ["of great value"]).

***Amphithecium prodotum* sp. n.**
(Figs. 77, 103–110)

TYPE HOST AND LOCALITY: *Pristobrycon striolatus*: Rio Capucapú at its confluence with Rio Jatapú, Cachoeira das Garças, Amazonas (31 October 1989).

OTHER RECORDS: *Catoprion mento*: Balbina, Rio Uatumã, Amazonas (20 September 1985);

Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Rio Uatumã, Lago Tapaná, near Santana, Amazonas (3 November 1989). *Pristobrycon striolatus*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Santa Luzia, Rio Uatumã, Amazonas (20 September 1985); Lago Samaumá, Rio Uatumã, Amazonas (25 September 1985); Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas (26 November 1984).

SPECIMENS STUDIED: Holotype, INPA PLH 263; 28 paratypes, INPA PLH 329, PLH 330, USNPC 85841, 85842, 85843, 85844, HWML 38597 from *P. striolatus*; 25 vouchers, USNPC 85845, 85846, 85847 from *C. mento*.

COMPARATIVE MEASUREMENTS: Dimensions of specimens from *C. mento* follow those of *P. striolatus* in brackets.

DESCRIPTION: Body fusiform, with slight constriction near midlength; length 248 (202–349; $n = 15$) [245 (219–280; $n = 5$)], greatest width 70 (60–93; $n = 16$) [65 (52–73; $n = 5$)] in anterior or posterior trunk. Tegument smooth. Cephalic lobes moderately developed. Eyes 4; posterior members with lens, larger, slightly farther apart than anterior pair; accessory granules absent or few in cephalic, anterior trunk regions. Pharynx spherical, 15 (13–17; $n = 17$) [14 (13–16; $n = 4$)] in diameter. Peduncle broad; haptor 50 (44–68; $n = 16$) [49 (43–59; $n = 5$)] long, 65 (58–75; $n = 15$) [63 (57–68; $n = 4$)] wide. Anchors similar; each with elongate slightly depressed superficial root, prominent deep root, slightly curved shaft, long point; ventral anchor 29 (25–31; $n = 10$) [30 (29–32; $n = 10$)] long, base 12 (11–13; $n = 8$) [12 (11–14; $n = 7$)] wide; dorsal anchor 30 (26–33; $n = 9$) [31 (30–33; $n = 6$)] long, base 13 (11–14; $n = 8$) [14 (12–15; $n = 6$)] wide. Ventral bar 27 (25–29; $n = 11$) [28 (27–29; $n = 3$)] long, slightly bent at midlength, with enlarged terminations; dorsal bar 24 (22–26; $n = 14$) [24–25 ($n = 3$)] long, broadly U-shaped, ends directed laterally. Hook pair 1—15 (14–16; $n = 8$) [16 (14–17; $n = 8$)], pairs 2, 6—17 (16–19; $n = 13$) [19 (17–20; $n = 11$)], pair 3—20 (19–22; $n = 7$) [21 (19–23; $n = 8$)], pairs 4, 7—23 (21–26; $n = 14$) [25 (22–27; $n = 19$)], pair 5—13 ($n = 4$) [13–14 ($n = 4$)] long. Copulatory organ 22 (20–24; $n = 6$) [21 (20–23; $n = 8$)] long, rapidly tapered to broad tube; base with sclerotized margin. Distal rod of accessory piece 19 (18–21; $n = 6$) [19 (17–22; $n = 8$)] long, straight, with terminal hook, indistinct thumb. Gonads pyriform to su-

bovate; testis 40 (35–44; $n = 5$) [44 (41–46; $n = 2$)] long, 20 (18–21; $n = 5$) [20 (16–24; $n = 2$)] wide; germarium 44 (34–62; $n = 6$) [50 (41–64; $n = 3$)] long, 18 (15–21; $n = 6$) [20 (18–23; $n = 3$)] wide. Ootype, oviduct, uterus not observed; vaginae slightly distended; seminal receptacle small; vitellaria dense throughout trunk except absent in areas of reproductive organs.

REMARKS: *Amphithecium prodotum* resembles *A. muricatum* and *A. minutum* in comparative morphology of the haptoral armament. Features distinguishing it from these species are presented in the remarks for the latter 2 species. The specific name is from Greek (*prodotos* ["betrayed"]).

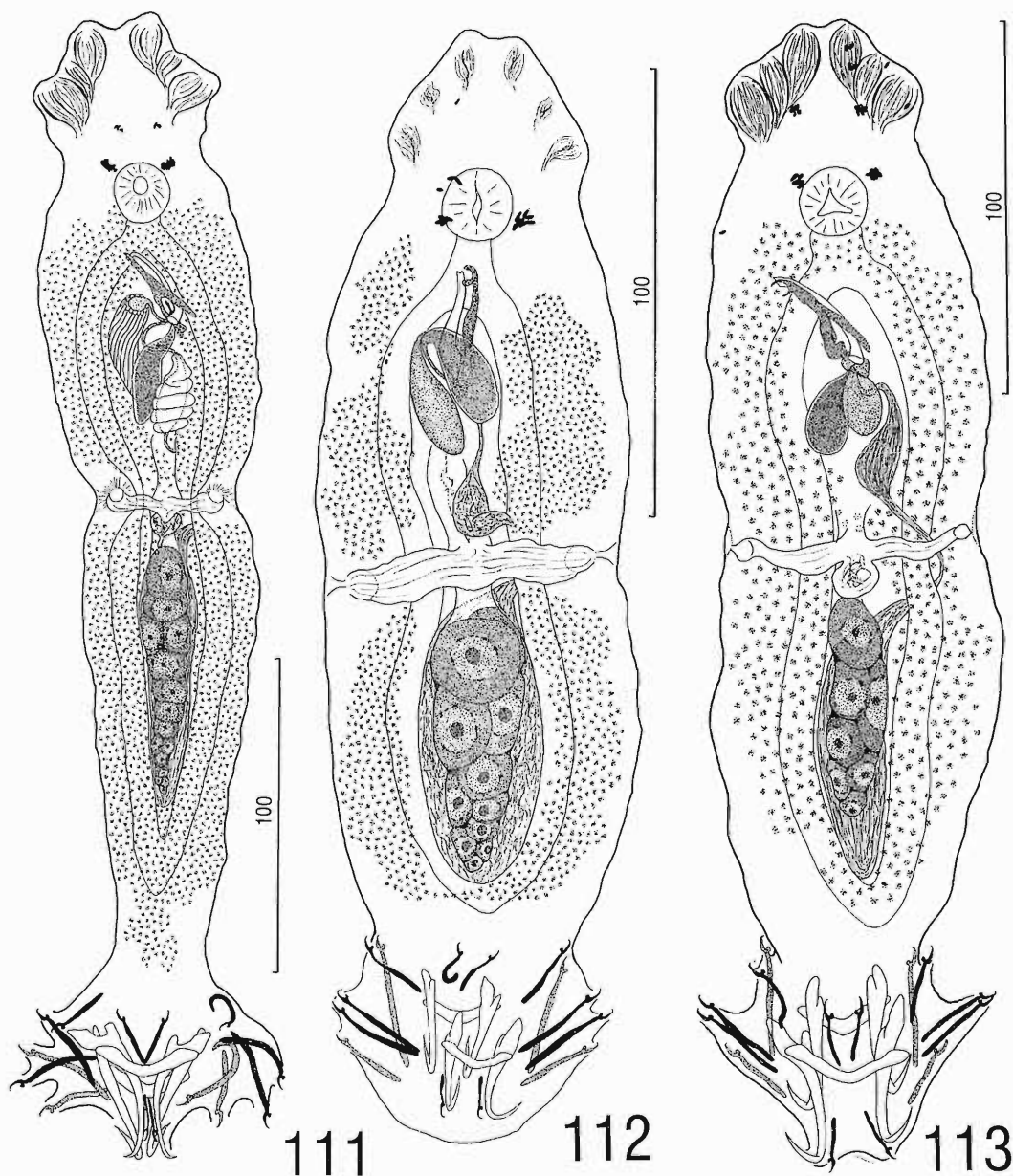
Amphithecium speirocamarotum sp. n.

(Figs. 111, 114–121)

TYPE HOST AND LOCALITY: *Serrasalmus elongatus*: Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas (26 November 1984).

SPECIMENS STUDIED: Holotype, INPA PLH 250; 13 paratypes, INPA PLH 251, USNPC 85848, HWML 38598.

DESCRIPTION: Body 338 (290–364; $n = 8$) long, slender, constricted near midlength; posterior trunk tapered posteriorly; greatest width 75 (64–89; $n = 9$) in anterior trunk. Cephalic lobes well developed. Tegument smooth. Eyes 4 or anterior members absent; posterior members larger, slightly farther apart than anterior pair (when present); accessory granules absent or few in cephalic, anterior trunk regions. Pharynx spherical, 16 (15–18; $n = 9$) in diameter. Peduncle narrow; haptor 65 (60–72; $n = 8$) long, 87 (69–104; $n = 8$) wide. Anchors similar; each with elongate slightly depressed superficial root, prominent deep root, curved elongate shaft, short point; ventral anchor 47 (45–48; $n = 5$) long, base 15 (14–16; $n = 4$) wide; dorsal anchor 42 (39–44; $n = 5$) long, base 16 (15–18; $n = 3$) wide. Ventral bar 37 (35–40; $n = 4$) long, bent at midlength, with enlarged terminations; dorsal bar 34 (32–35; $n = 5$) long, broadly U-shaped, with terminal enlargements, ends developed laterally. Hook pairs 1, 2, 6—24 (21–28; $n = 11$), pair 3—28 (22–33; $n = 3$), pairs 4, 7—34 (31–38; $n = 8$), pair 5—16 (14–17; $n = 2$) long. Copulatory organ 30–31 ($n = 3$) long, with 2 rami; primary ramus recurved distally; short secondary ramus heavily sclerotized, blind; base with proximal flap. Distal rod of accessory piece 33 (32–35; $n = 3$) long, straight, with slightly recurved pointed tip, short thumb. Gonads pyr-

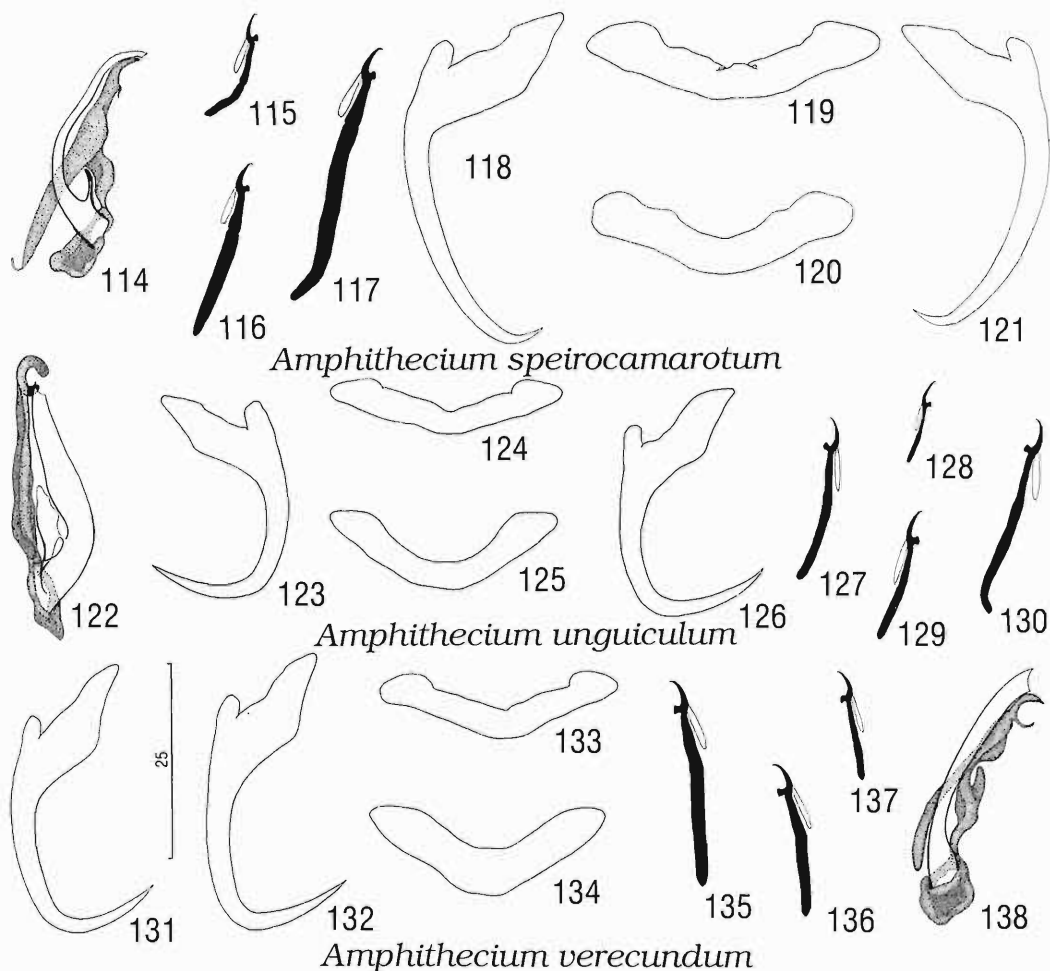


Figures 111–113. Whole-mount illustrations of *Amphothecium* spp. (composite, ventral views). 111. *Amphothecium speirocamarotum* sp. n. 112. *Amphothecium unguiculum* sp. n. 113. *Amphothecium verecundum* sp. n. (from *Pristobrycon eigenmanni*). All drawings are to respective 100- μ m scales.

iform. Testis 59 (52–68; $n = 6$) long, 21 (14–25; $n = 6$) wide; seminal vesicle with externally coiled wall; wall of dextral prostatic reservoir with spiraled muscles. Germarium 67 (57–91; $n = 8$) long, 22 (16–28; $n = 8$) wide; ootype not observed; vaginae distended slightly; seminal receptacle

small. Vitellaria dense throughout trunk except absent in areas of reproductive organs.

REMARKS: *Amphothecium speirocamarotum* is identified readily by the seminal vesicle with an externally coiled wall, the heavily sclerotized reduced secondary ramus of the copulatory or-



Figures 114–138. Sclerotized structures of *Amphithecium* spp. 114–121. *Amphithecium speirocamarotum* sp. n. 114. Copulatory complex (dorsal view). 115. Hook pair 5. 116. Hook pair 2. 117. Hook pair 7. 118. Ventral anchor. 119. Ventral bar. 120. Dorsal bar. 121. Dorsal anchor. 122–130. *Amphithecium unguiculum* sp. n. 122. Copulatory complex (ventral view). 123. Ventral anchor. 124. Ventral bar. 125. Dorsal bar. 126. Dorsal anchor. 127. Hook pair 2. 128. Hook pair 5. 129. Hook pair 1. 130. Hook pair 7. 131–138. *Amphithecium verecundum* sp. n. (from *Pristobrycon eigenmanni*). 131. Ventral anchor. 132. Dorsal anchor. 133. Ventral bar. 134. Dorsal bar. 135. Hook pair 7. 136. Hook pair 2. 137. Hook pair 5. 138. Copulatory complex (dorsal view). All drawings are to the 25- μ m scale.

gan, the spiraled muscles in the wall of the dextral prostatic reservoir, and the noticeably tapered peduncle. The specific name is from Greek (*speira* ["anything wrapped round"] + *kamarotos* ["vaulted"]) and refers to the wall of the seminal vesicle.

***Amphithecium unguiculum* sp. n.**
(Figs. 112, 122–130)

TYPE HOST AND LOCALITY: *Serrasalmus spilopleura*: Rio Uatumã, Lago Tapanã, near Santana, Amazonas (3 November 1989).

OTHER RECORD: *Serrasalmus spilopleura*: Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas (14 September 1984).

SPECIMENS STUDIED: Holotype, INPA PLH 252; 26 paratypes, INPA PLH 253, PLH 254, USNPC 85849, 85850, HWML 38599.

DESCRIPTION: Body 240 (201–298; $n = 10$) long, fusiform, slightly constricted near mid-length; greatest width 81 (56–104; $n = 11$) in anterior or posterior trunk. Tegument smooth or with scaled annulations. Cephalic lobes moder-

ately developed. Eyes 2, 4, or absent, anterior pair usually absent; each eye comprised of few, frequently dissociated granules; accessory granules common in cephalic, anterior trunk regions. Pharynx spherical, 16 (15–17; $n = 11$) in diameter. Peduncle broad; haptor 50 (41–67; $n = 10$) long, 69 (60–81; $n = 10$) wide. Anchors similar; each with well-developed roots, curved shaft, elongate point; ventral anchor 29 (28–30; $n = 13$) long, base width 12 (10–14; $n = 13$); dorsal anchor 31 (30–33; $n = 12$) long, base width 13 (11–16; $n = 12$). Bars similar, broadly U- or V-shaped, with slightly enlarged ends; ventral bar 27 (24–28; $n = 9$) long; dorsal bar 26 (24–28; $n = 9$) long. Hook pairs 1, 6–18 (16–19; $n = 23$); pair 2–20 (18–23; $n = 9$); pairs 3, 4–25 (23–28; $n = 24$); pair 5–13–14 ($n = 10$); pair 7–28 (25–31; $n = 15$) long. Copulatory organ 35 (33–36; $n = 9$) long, with proximal bend, submedial dilation, 2 rami; primary ramus broad; secondary ramus flattened, blind; base with sclerotized margin, short proximal flap. Accessory piece 29 (27–32; $n = 13$) long, blunt, with rod incorporated into articulation process, C-shaped terminally. Testis 53 (29–75; $n = 8$) long, 23 (14–31; $n = 8$) wide, subovate. Germarium conical, 46 (27–73; $n = 10$) long, 20 (12–28; $n = 10$) wide; oviduct short; ootype not observed; vaginae dilated; vitellaria in bilateral fields of anterior, posterior trunk, absent in regions of reproductive organs.

REMARKS: This species resembles *Amphithecium falcatum* by lacking a free distal rod of the accessory piece and in the general morphology of haptoral sclerites. *Amphithecium unguiculum* differs from *A. falcatum* in the comparative morphology of the copulatory organ. The secondary ramus is reduced and flattened and the primary ramus is inflated in *A. unguiculum*, whereas the primary ramus is flattened and the secondary ramus fine and elongate in *A. falcatum*. The specific name is from Latin (*unguiculus* [“a small talon or claw”]) and refers to the end of the accessory piece.

***Amphithecium verecundum* sp. n.**
(Figs. 113, 131–138)

TYPE HOST AND LOCALITY: *Pristobrycon eigenmanni*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

OTHER RECORDS: *Pristobrycon eigenmanni*: Nazaré, Rio Uatamá, Amazonas (17 September 1985); Rio Negro near Manaus, Amazonas (28

December 1988). *Serrasalmus* sp. (2 of Jégu): Rio Uatamá, Lago Tapaná, near Santana, Amazonas (3 November 1989).

SPECIMENS STUDIED: Holotype, INPA PLH 248; 16 paratypes, INPA PLH 249, USNPC 85851, 85852, 85853, HWML 38600 from *Pristobrycon eigenmanni*; 3 vouchers from *Serrasalmus* sp. (2 of Jégu), USNPC 85854.

COMPARATIVE MEASUREMENTS: Measurements of specimens from *Serrasalmus* sp. (2 of Jégu) are in brackets following those of the type series.

DESCRIPTION: Body fusiform, with slight narrowing at midlength; length 267 (205–310; $n = 10$), greatest width 73 (59–84; $n = 10$) in anterior or posterior trunk. Tegument smooth or with scaled annulations. Cephalic lobes moderately developed. Eyes 4, equidistant; posterior members larger, farther apart than anterior pair; few accessory granules in cephalic, anterior trunk regions. Pharynx spherical, 16 (12–20; $n = 11$) in diameter. Peduncle broad; haptor 59 (51–78; $n = 10$) long, 70 (55–77; $n = 9$) wide. Anchors similar; each with well-developed slightly depressed superficial root, short deep root, straight shaft, elongate point; ventral anchor 35 (34–36; $n = 6$) [34–35 ($n = 3$)] long, base 12 (11–14; $n = 6$) [13 (11–14; $n = 3$)] wide; dorsal anchor 36 (35–37; $n = 6$) [35 (33–36; $n = 3$)] long, base 13–14 ($n = 6$) [13 (12–14; $n = 3$)] wide. Ventral bar 28 (24–30; $n = 10$) long, broadly V-shaped, with enlarged terminations; dorsal bar 28 (27–29; $n = 6$) long, broadly U-shaped. Hook pairs 1, 2–20 (19–21; $n = 11$) [19 (18–20; $n = 5$)], pair 3–24 (23–28; $n = 5$) [21 (20–22; $n = 3$)], pairs 4, 7–27 (25–29; $n = 12$) [25 (23–26; $n = 5$)], pair 5–15 (14–17; $n = 5$) [19 ($n = 1$)], pair 6–21 (18–23; $n = 6$) [19–20 ($n = 2$)] long. Copulatory organ 31 (30–34; $n = 4$) [32 (31–33; $n = 2$)] long, arcuate, with slight narrowing distal to base; base with short proximal flap. Distal rod of accessory piece 26 (25–29; $n = 5$) [24 (22–27; $n = 20$)] long, with distal C-shaped hook, lower arm of hook delicate. Testis fusiform, 47 (38–56; $n = 3$) long, 24 (23–25; $n = 3$) wide. Germarium irregular, 50 (42–57; $n = 6$) long, 17 (12–24) wide; oviduct, ootype not observed; vaginae conspicuous; seminal receptacle small or absent; vitellaria throughout trunk except absent in regions of reproductive organs.

REMARKS: The copulatory complex of this species resembles that of *Amphithecium prodo-*

tum by having a single ramus of the copulatory organ and a hook-like termination of the accessory piece. It differs from this species by the lower arm of the C-shaped hook being relatively long and delicate. The species name is from Latin (*verecundus* ["unassuming"]).

Heterothecium gen. n.

DIAGNOSIS: Body fusiform, comprising cephalic region, trunk, peduncle, haptor. Tegument thin, smooth or with scaled annulations. Two terminal, 2 bilateral cephalic lobes; head organs, unicellular cephalic glands present. Four eyes; granules elongate ovate. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus short; intestinal ceca 2, confluent posterior to testis, lacking diverticula. Gonads intercecal, overlapping; testis dorsal to germarium. Vas deferens looping left intestinal cecum; seminal vesicle sigmoid, a dilation of vas deferens. Two prostatic reservoirs saccate. Genital pore midventral near level of cecal bifurcation. Copulatory complex comprising articulated copulatory organ, accessory piece; copulatory organ tubular, with 2 subequal rami opening terminally; distal rod of accessory piece, proximal articulation process present. Vagina of soft tissue; vaginal pore sinistrodorsal; vaginal vestibule lightly sclerotized. Seminal receptacle small or absent. Haptor subhexagonal; with pairs of dorsal and ventral anchor/bar complexes, 7 pairs of similar hooks with ancyrocephaline distribution. Each hook with delicate point, truncate protruding thumb, expanded shank comprising 2 subunits; proximal subunit variable in length between hook pairs; FH loop extending to union of shank subunits. Ventral bar lacking antero-medial projection. Parasites of gills of serrasalmid fishes.

TYPE SPECIES: *Heterothecium globatum* sp. n. from *Serrasalmus gouldingi*.

OTHER SPECIES: *Heterothecium dicrophallum* sp. n. from *Catoprion mento*.

REMARKS: *Heterothecium* is characterized by the combined presence in its member species of a sinistrodorsal vaginal pore, a sclerotized vaginal vestibule, and a male copulatory organ with 2 rami, and absence of development of the distal end on the articulation process of the accessory piece. *Pithanothecium*, its apparent sister taxon, includes species possessing a dextrolateral vaginal aperture and a blunt articulation process extending past the distal rod of the ac-

cessory piece. The generic name is from Greek (*hetero* ["different"] + *theke* ["a small case"]).

Heterothecium globatum sp. n.

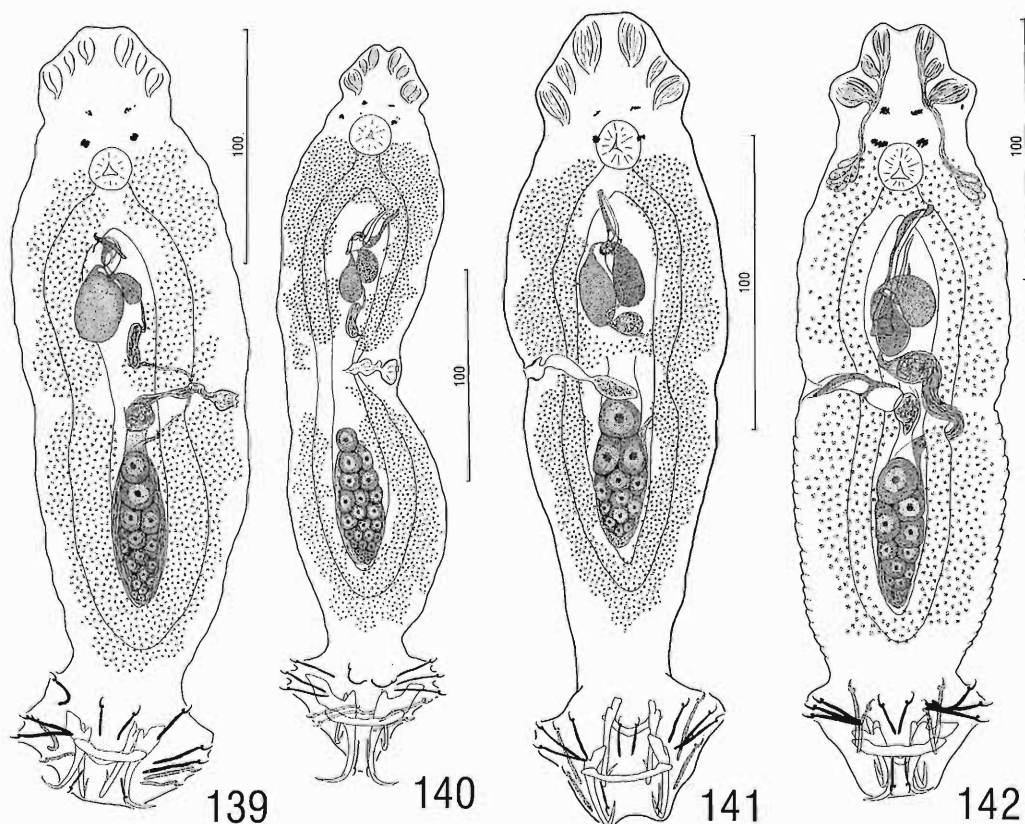
(Figs. 139, 143–152)

TYPE HOST AND LOCALITY: *Serrasalmus gouldingi*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989).

OTHER RECORD: *Serrasalmus gouldingi*: C. Miriti, Rio Uatumã, Amazonas (20 September 1985).

SPECIMENS STUDIED: Holotype, INPA PLH 303; 22 paratypes, INPA PLH 304, PLH 305, USNPC 85869, 85870, HWML 38601.

DESCRIPTION: Body fusiform, 326 (310–361; $n = 7$) long; greatest width 89 (75–103; $n = 9$) usually in anterior trunk. Tegument frequently with scaled annulations. Cephalic lobes moderately developed. Eyes 4; posterior pair larger, farther apart than anterior pair; accessory granules usually absent, occasionally in cephalic, anterior trunk regions. Pharynx spherical, 17 (16–19; $n = 9$) in diameter. Peduncle broad; haptor 59 (52–67; $n = 9$) long, 78 (69–87; $n = 9$) wide. Anchors similar; each with elongate depressed superficial root, prominent deep root, slightly curved shaft, elongate point. Ventral anchor 34 (33–36; $n = 12$) long, base 13 (12–14; $n = 9$) wide; dorsal anchor 29 (28–31; $n = 11$) long, base 11 (9–12; $n = 7$) wide. Ventral bar 31 (29–32; $n = 8$) long, with indistinct bend at midlength, enlarged ends; dorsal bar 24 (23–25; $n = 8$) long, broadly V-shaped, with slightly enlarged ends. Hook pairs 1, 5–14–15 ($n = 17$), pair 2–17 (16–19; $n = 8$), pair 3–20 (19–21; $n = 10$), pair 4–22 (21–23; $n = 9$), pair 6–16 (15–17; $n = 5$), pair 7–19 (16–20; $n = 9$) long. Copulatory organ 28 (24–34; $n = 9$) long; primary ramus arced with small bulbous end; secondary ramus straight with broad termination; base with sclerotized margin, short proximal flap. Distal rod of accessory piece 20 (17–23; $n = 8$) long, terminally acute; articulation process twisted. Gonads subovate; testis 61 (55–66; $n = 3$) long, 27 (25–29; $n = 3$) wide; germarium 63 (51–73; $n = 4$) long, 21 (16–25; $n = 4$) wide. Seminal vesicle lying to left of midline, a short dilated dextroventral loop of vas deferens. Oviduct, ootype, uterus not observed; seminal receptacle small near midlength, apparently representing proximal dilation of vagina; vaginal pore irregular, vestibule lightly sclerotized; vitel-



Figures 139–142. Whole-mount illustrations of *Heterothecium* spp. and *Pithanothecium* spp. (composite, ventral views). 139. *Heterothecium globatum* sp. n. 140. *Heterothecium dicrophallum* sp. n. 141. *Pithanothecium piranhus* (Mizelle and Price, 1965) comb. n. (from *Pygopristis denticulata*). 142. *Pithanothecium amazonensis* (Mizelle and Price, 1965) comb. n. (from *Pristobrycon striolatus*). All drawings are to respective 100- μ m scales.

laria limited to trunk, absent in regions of reproductive organs.

REMARKS: This species differs from *Heterothecium dicrophallum* in the comparative morphology of the copulatory complexes and by having a V-shaped dorsal bar (U-shaped in *H. dicrophallum*) and anchors of similar size (dorsal anchor about $\frac{1}{2}$ length of ventral anchor in *H. dicrophallum*). The specific name is from Latin (*globatus* [“to make into a ball”]) and refers to the termination of the primary ramus of the copulatory organ.

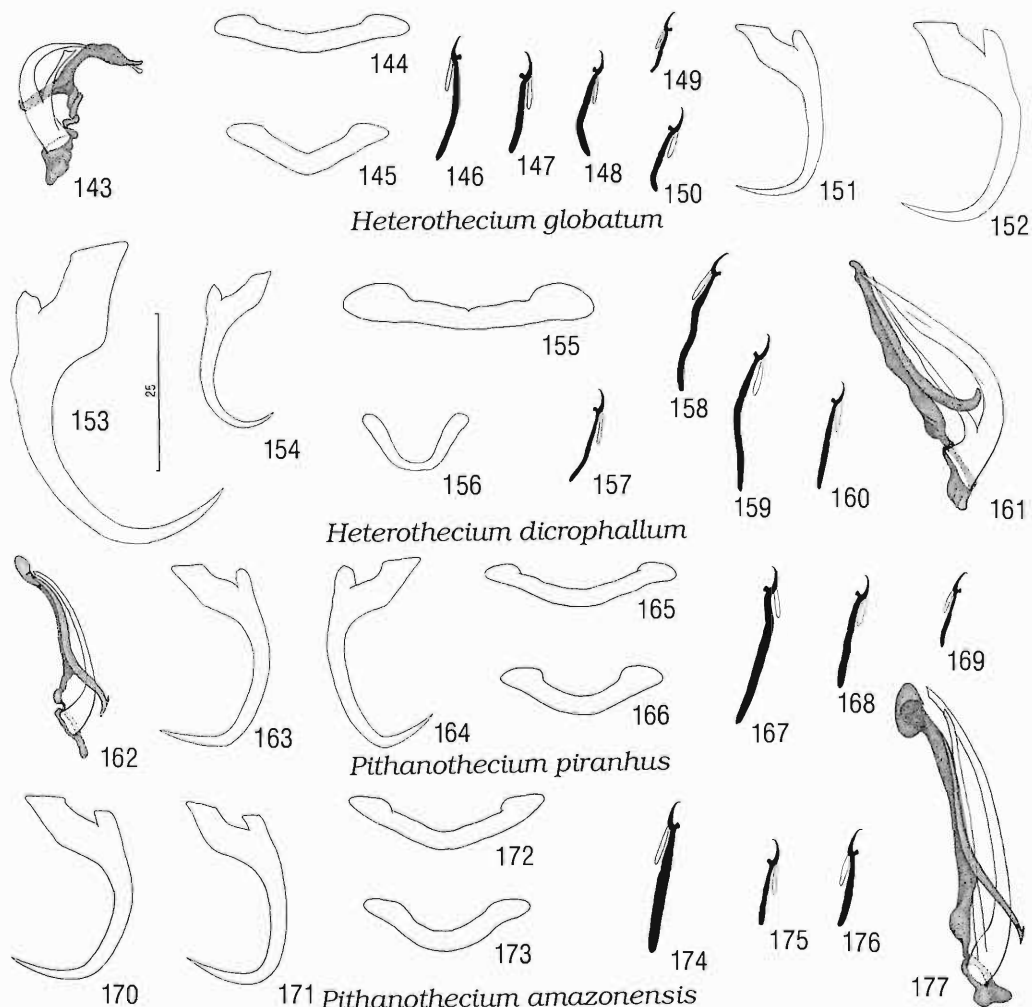
***Heterothecium dicrophallum* sp. n.**
(Figs. 140, 153–161)

TYPE HOST AND LOCALITY: *Catoprion mento*: Balbina, Rio Uatumã, Amazonas (20 September 1985).

OTHER RECORD: *Catoprion mento*: Rio Uatumã, Lago Tapanã, near Santana, Amazonas (3 November 1989).

SPECIMENS STUDIED: Holotype, INPA PLH 306; 22 paratypes, INPA PLH 307, PLH 331, USNPC 85871, 85872, HWML 38602.

DESCRIPTION: Body 356 (318–386; $n = 10$) long, fusiform, with slight to obvious constriction near midlength; greatest width 76 (60–93; $n = 8$) in anterior or posterior trunk. Tegument smooth. Cephalic lobes moderately developed. Eyes 4, poorly organized; posterior pair larger, farther apart than anterior pair; granules variable in size; accessory granules usually present in cephalic, anterior trunk regions. Pharynx spherical, 20 (18–22; $n = 8$) in diameter. Peduncle broad; haptor 71 (64–77; $n = 9$) long, 81 (79–85; $n = 8$) wide. Ventral anchor 47 (46–49; $n = 8$) long,



Figures 143–177. Sclerotized structures of *Heterothecium* spp. and *Pithanothecium* spp. 143–152. *Heterothecium globatum* sp. n. 143. Copulatory complex (dorsal view). 144. Ventral bar. 145. Dorsal bar. 146. Hook pair 4. 147. Hook pair 2. 148. Hook pair 7. 149. Hook pair 5. 150. Hook pair 1. 151. Dorsal anchor. 152. Ventral anchor. 153–161. *Heterothecium dicrophallum* sp. n. 153. Ventral anchor. 154. Dorsal anchor. 155. Ventral bar. 156. Dorsal bar. 157. Hook pair 5. 158. Hook pair 2. 159. Hook pair 7. 160. Hook pair 1. 161. Copulatory complex (ventral view). 162–169. *Pithanothecium piranhus* (Mizelle and Price, 1965) comb. n. (from *Pygopristis denticulata*). 162. Copulatory complex (ventral view). 163. Ventral anchor. 164. Dorsal anchor. 165. Ventral bar. 166. Dorsal bar. 167. Hook pair 7. 168. Hook pair 2. 169. Hook pair 5. 170–177. *Pithanothecium amazonensis* (Mizelle and Price, 1965) comb. n. (from *Pygopristis denticulata*). 170. Ventral anchor. 171. Dorsal anchor. 172. Ventral bar. 173. Dorsal bar. 174. Hook pair 7. 175. Hook pair 5. 176. Hook pair 2. 177. Copulatory complex (ventral view). All drawings are to the 25- μ m scale.

with depressed superficial root, short deep root, prominent ventral hump on base, evenly curved shaft, elongate point; base 20 (17–21; $n = 6$) wide. Dorsal anchor 25 (24–27; $n = 7$) long, with well-developed roots, evenly curved shaft, point; base 9–10 ($n = 5$) wide. Ventral bar 41 (40–42; $n = 5$) long, straight to slightly bent,

with enlarged terminations; dorsal bar 20 (18–23; $n = 5$) long, U-shaped, with slightly enlarged ends. Hook pair 1–19–20 ($n = 5$), pair 2–26 (24–27; $n = 4$), pair 3–27 (25–29; $n = 7$), pairs 4, 7–30 (28–32; $n = 11$), pair 5–17–18 ($n = 4$), pair 6–21 (20–22; $n = 6$) long. Copulatory organ 42 (36–50; $n = 10$) long; pri-

mary ramus broad, expanded distally; secondary ramus slender, pointed; base with sclerotized margin, short proximal flap. Distal rod of accessory piece 32 (26–35; $n = 9$) long, curved, with terminal stout hook. Gonads subovate; testis 62 (61–63; $n = 2$) long, 21 (16–26; $n = 2$) wide; germarium 57 (46–75; $n = 8$) long, 21 (16–26; $n = 7$) wide. Seminal vesicle lying to left of midline, a short dilated dextroventral loop of vas deferens. Oviduct, ootype, uterus, seminal receptacle not observed. Vagina slightly dilated; vestibule lightly sclerotized. Vitellaria limited to trunk, absent in regions of reproductive organs and near body midlength.

REMARKS: Characters differentiating *Heterothecium dicrophallum* from *H. globatum* are presented in the Remarks section for the latter species. The specific name is from Greek (*dikroos* ["forked"] + *phallos* ["the penis"]).

Pithanothecium gen. n.

DIAGNOSIS: Body fusiform, comprising cephalic region, trunk, peduncle, haptor. Tegument thin, with scaled annulations. Two terminal, 2 bilateral cephalic lobes; head organs present; unicellular cephalic glands lying dorsolateral to pharynx. Eyes 4; granules elongate ovate. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus short; 2 intestinal ceca confluent posterior to gonads, lacking diverticula. Gonads intercecal, overlapping; testis dorsal to germarium. Vas deferens looping left intestinal cecum; seminal vesicle lying near or slightly sinistral to body midline, a sigmoid dilation of vas deferens. Two saccate prostatic reservoirs; prostates comprising glandular areas lying dorsal to anterior portions of ceca. Genital pore midventral at level of cecal bifurcation. Copulatory complex comprising articulated copulatory organ, accessory piece; copulatory organ tubular with 1 or 2 subequal rami opening terminally; accessory piece with distal rod, proximal articulation process extending distal to tip of rod as small blunt flap. Vagina nonsclerotized; vaginal aperture simple, dextrolateral near body midlength; vaginal vestibule present, with sclerotized wall. Seminal receptacle lying on midline anterior to germarium. Haptor subhexagonal; with dorsal and ventral anchor/bar complexes, 7 pairs of similar hooks with ancyrocephaline distribution. Anchors similar, unmodified. Ventral bar lacking anteromedial projection. Hook with truncate protruding thumb,

delicate point, expanded shank comprising 2 subunits; proximal subunit variable in length between hook pairs. FH loop extending to union of shank subunits. Parasites of gills of serrasalmid fishes.

TYPE SPECIES: *Pithanothecium piranhus* (Mizelle and Price, 1965) comb. n. from *Catoprion mento*, *Pristobrycon striolatus*, *Pygocentrus nattereri* (type host), and *Pygopristis denticulata*.

OTHER SPECIES: *Pithanothecium amazonensis* (Mizelle and Price, 1965) comb. n. from *Catoprion mento*, *Pristobrycon striolatus*, *Pygocentrus nattereri* (type host), and *Pygopristis denticulata*.

REMARKS: Features distinguishing *Pithanothecium* from other genera in the complex of ancyrocephaline species infesting serrasalmids include presence of a sclerotized vaginal vestibule opening on the dextrolateral surface of the trunk and the distally blunt articulation process of the accessory piece extending past the tip of the distal rod. It is separated from *Heterothecium*, its apparent sister genus in position of the vaginal aperture (dextrolateral in *Pithanothecium*; sinistrolateral in *Heterothecium*). The generic name is from Greek (*pithanos* ["probable"] + *theke* ["a small case"]).

Pithanothecium piranhus (Mizelle and Price, 1965) comb. n. (Figs. 141, 162–169)

SYNONYM: *Cleidodiscus piranhus* Mizelle and Price, 1965.

RECORDS: *Catoprion mento*: Rio Uatumã, Lago Tapaná, Santana, Amazonas (3 November 1989); Rio Jatapú, Lago Maracana, Amazonas (2 November 1989). *Pristobrycon striolatus*: Rio Jatapú, Lago Maracana, Amazonas (2 November 1989). *Pygocentrus nattereri*: Rio Uatumã, Lago Tapaná, Santana, Amazonas (3 November 1989). *Pygopristis denticulata*: Rio Uatumã, Lago Tapaná, Santana, Amazonas (3 November 1989); Rio Xingu, Parana Maxipanã, Pará (17, 18 October 1992); Rio Araguari, Lago Compri-do, Amapá (15 August 1992).

PREVIOUS RECORD: *Pygocentrus nattereri* (type host): Amazon River (type locality). The original host was obtained from Steinhart Aquarium, San Francisco, California (Mizelle and Price, 1965).

SPECIMENS STUDIED: Holotype, paratype, voucher from *Pygocentrus nattereri*, USNPC

Table 6. Comparative measurements (in micrometers) of *Pithanothecium piranhus* (Mizelle and Price, 1965) comb. n., from 4 serrasalmid hosts.

	<i>Catoprion mento</i>	N	<i>Pristobrycon striolatus</i>	N	<i>Pygocentrus nattereri</i>	N*	<i>Pygopristis denticulata</i>	N
Body								
Length	277 (252–303)	3	250 (236–270)	6	—	—	250 (187–285)	12
Width	89 (83–92)	3	66 (62–72)	6	—	—	74 (61–83)	12
Haptor								
Length	59–60	3	49 (44–59)	6	—	—	54 (45–69)	11
Width	81 (70–93)	3	70 (59–75)	6	—	—	70 (63–78)	11
Pharynx								
Diameter	17 (16–18)	3	16–17	7	—	—	16 (13–17)	12
Copulatory organ								
Length	32 (30–35)	7	32–33	2	31	1	30 (24–32)	27
Accessory piece								
Length	29 (25–32)	8	29–30	2	28	1	28 (24–30)	29
Dorsal anchor								
Length	34 (32–37)	9	32	2	33 (32–35)	2	31 (29–33)	23
Base width	14 (12–16)	5	13–14	2	12 (11–14)	2	14 (12–15)	21
Ventral anchor								
Length	32 (31–34)	9	30	1	30	2	29 (27–31)	26
Base width	12 (10–14)	7	12	1	10	2	12 (10–14)	25
Bar length								
Dorsal	28–29	3	26 (25–27)	6	—	—	27 (26–28)	9
Ventral	33 (32–34)	3	30 (28–31)	6	—	—	31 (29–32)	9
Hook lengths								
Pair 1	18	3	19	1	17–18	2	17 (16–19)	17
Pair 2	20 (19–21)	7	20	1	19	2	19 (17–20)	14
Pair 3	23 (22–25)	6	23 (22–24)	2	22	2	21 (20–23)	19
Pair 4	26 (25–27)	7	25	1	25–26	2	24–25	14
Pair 5	13–14	3	—	—	13	1	13 (12–14)	8
Pair 6	19 (18–20)	5	19–20	2	18–19	2	18 (16–19)	10
Pair 7	28 (27–29)	7	27–28	2	26–27	2	25 (24–28)	19
Germarium								
Length	40 (39–43)	3	39	1	—	—	46 (33–56)	7
Width	17 (16–19)	3	19	1	—	—	15 (13–17)	7
Testis								
Length	37 (36–39)	3	40 (38–43)	2	—	—	41 (30–50)	5
Width	20 (18–21)	3	16 (15–17)	2	—	—	16 (10–21)	5

* Measurements of the holotype and paratype are not included.

60463, HWML 21290, USNPC 85863, respectively; 14 vouchers from *Catoprion mento*, USNPC 85864, 85865; 9 vouchers from *Pristobrycon striolatus*, USNPC 85862; 47 vouchers from *Pygopristis denticulata*, USNPC 85866, 85867, 85868.

COMPARATIVE MEASUREMENTS: Table 6.

REDESCRIPTION: Greatest body width usually in anterior trunk. Tegumental annulations, scales poorly developed, peduncular, absent in most specimens. Cephalic lobes moderately to poorly

developed; cephalic glands not observed. Eyes equidistant or anterior pair closer together, smaller than posterior pair; accessory granules absent to numerous in cephalic, anterior trunk regions. Pharynx spherical. Peduncle broad. Each anchor with well-developed roots, slightly depressed superficial root, evenly curved shaft, elongate point. Ventral bar rod-shaped, slightly bent near midlength, with terminal enlargements; dorsal bar broadly U-shaped, with enlarged ends. Copulatory organ arcuate, tapered;

base with small proximal flap. Distal rod of accessory piece sigmoid; terminal flap of articulation process globose. Gonads subovate to pyriform; oviduct, ootype not observed; wall of vaginal vestibule thickened; seminal receptacle ovate to pyriform; vitellaria distributed throughout trunk except absent in regions of reproductive organs.

REMARKS: This species has not been reported since its original description from *Pygocentrus nattereri* by Mizelle and Price (1965), who assigned it to *Cleidodiscus* on the basis of the basally articulated copulatory organ and accessory piece. Beverley-Burton and Suriano (1980) redefined *Cleidodiscus* and provided a redescription of the type species, *C. robustus*, but refrained from commenting on the generic status of the many other described species then assigned to the genus. With the exceptions of *C. brachus* and *C. venardi* (see Beverley-Burton, 1984), other described species of *Cleidodiscus* have been generally considered incertae sedis or have been reassigned within the Ancyrocephalinae.

Kritsky and Thatcher (1983) suggested that the monogenoideans described by Mizelle and Price (1965) from *Pygocentrus nattereri* were members of undefined Neotropical genera. Our rediscovery of *Cleidodiscus piranhus* confirms that it should be reassigned, for which we propose it as the type species of *Pithanothecium* gen. n. Mizelle and Price (1965) considered the vagina to be absent in their specimens. Although vaginae cannot be seen in the unstained holotype and paratype, comparative morphology of haptor and copulatory sclerites confirms the conspecificity of our specimens. This species differs from *Pithanothecium amazonensis*, its only congener, by possessing a delicate vaginal tube and vestibule, a single ramus of the copulatory organ, and a small terminal flap of the articulation process of the accessory piece and in the comparative morphology of the haptor armament.

Pithanothecium amazonensis
(Mizelle and Price, 1965) comb. n.
(Figs. 142, 170–177)

SYNONYM: *Cleidodiscus amazonensis* Mizelle and Price, 1965.

RECORDS: *Catoprion mento*: Rio Uatumã, Lago Tapanã, Santana, Amazonas (3 November 1989); Rio Jatapú, Lago Maracana, Amazonas

(2 November 1989); Balbina, Rio Uatumã, Amazonas (20 September 1985). *Pristobrycon striolatus*: Rio Capucapú at its confluence with Rio Jatapú, Cachoeira das Garças, Amazonas (31 October 1989); Rio Jatapú, Lago Maracana, Amazonas (2 November 1989); Lago Samaumã, Rio Uatumã, Amazonas (25 September 1985). *Pygopristis denticulata*: Rio Uatumã, Lago Tapanã, Santana, Amazonas (3 November 1989); Rio Araguari, Lago Comprido, Amapá (15 August 1992).

PREVIOUS RECORD: *Pygocentrus nattereri* (type host): Amazon River (type locality). The original host was obtained from Steinhart Aquarium, San Francisco, California (Mizelle and Price, 1965).

SPECIMENS STUDIED: Holotype, paratype from *Pygocentrus nattereri*, USNPC 60462, HWML 21289, respectively; 14 vouchers from *Catoprion mento*, USNPC 85859, 85860, 85861; 7 vouchers from *Pristobrycon striolatus*, USNPC 85855, 85856, 85965; 17 vouchers from *Pygopristis denticulata*, USNPC 85857, 85858.

COMPARATIVE MEASUREMENTS: Table 7.

REDESCRIPTION: Body slightly constricted near midlength; greatest width in anterior or posterior trunk. Scaled tegumental annulations in posterior trunk, peduncle. Cephalic lobes moderately developed. Anterior eyes slightly closer together, smaller than posterior pair; eye granules variable in size; accessory granules few or absent in cephalic, anterior trunk regions. Pharynx spherical. Peduncle broad. Each anchor with well-developed roots (superficial root slightly depressed), straight or slightly curved shaft, elongate point. Ventral bar rod-shaped, usually bent at midlength, with terminal enlargements; dorsal bar broadly U-shaped. Copulatory organ with 2 subequal rami with terminal openings; base with small proximal flap. Distal rod of accessory piece sigmoid; terminal flap of articulation process spatulate, with recurved end. Gonads subovate. Oviduct elongate; ootype, uterus not observed; vaginal vestibule extending to near midline, with sclerotized rib, ring; vaginal tube short to nonexistent; seminal receptacle small, pyriform, adjacent or slightly posterior to proximal end of vaginal vestibule; vitellaria in trunk, absent in regions of reproductive organs.

REMARKS: *Pithanothecium amazonensis* was originally described from *Pygocentrus nattereri* and placed in *Cleidodiscus* by Mizelle and Price (1965). Boeger and Kritsky (1988) provided an

Table 7. Comparative measurements (in micrometers) of *Pithantheceum amazonensis* (Mizelle and Price, 1965) comb. n., from 3 serrasalmid hosts.

	<i>Catoprion mento</i>	<i>N</i>	<i>Pristobrycon striolatus</i>	<i>N</i>	<i>Pygopristis denticulata</i>	<i>N</i>
Body						
Length	305 (246–336)	6	300 (268–330)	4	272 (247–291)	7
Width	98 (80–114)	6	103 (89–121)	4	101 (92–112)	8
Haptor						
Length	70 (55–75)	6	68 (59–75)	3	65 (53–72)	7
Width	85 (66–102)	6	81 (70–92)	3	83 (80–85)	7
Pharynx						
Diameter	18 (15–19)	6	18 (16–21)	4	18 (16–20)	8
Copulatory organ						
Length	56 (51–61)	8	51 (47–57)	3	54 (49–60)	8
Accessory piece						
Length	49 (47–53)	8	40 (32–57)	4	47 (40–51)	7
Dorsal anchor						
Length	37 (36–38)	7	38	2	33 (31–36)	5
Base width	14 (12–17)	2	16 (14–17)	2	13 (12–14)	4
Ventral anchor						
Length	34 (32–35)	7	36–37	2	31 (30–32)	6
Base width	16 (15–17)	5	13–14	2	14–15	6
Bar length						
Dorsal	32 (30–33)	3	31 (30–32)	4	30 (29–32)	7
Ventral	38 (37–39)	4	37 (35–38)	4	35 (32–36)	6
Hook lengths						
Pair 1	19–20	3	19	2	18 (17–20)	5
Pair 2	26 (25–29)	5	21	2	20 (19–21)	5
Pair 3	30 (29–32)	5	24–25	2	23 (21–25)	6
Pair 4	32 (30–34)	7	25 (24–27)	2	26 (24–27)	7
Pair 5	16 (15–17)	5	16	1	16–17	3
Pair 6	22–23	4	20–21	2	19 (18–20)	3
Pair 7	30 (28–33)	6	28–29	3	26 (24–28)	5
Germaurium						
Length	50 (43–57)	5	54 (45–68)	3	53 (47–60)	6
Width	26 (23–30)	5	21 (20–23)	3	22 (21–26)	6
Testis						
Length	55 (51–64)	5	61 (47–74)	2	54 (51–55)	4
Width	26 (21–33)	5	18 (17–19)	2	24 (17–28)	4

illustration of the copulatory complex from the holotype of *C. amazonensis* but suggested that the type host may have been originally misidentified. Records of dactylogyrids collected from serrasalmid hosts, including *P. nattereri*, during the present study, supports this assertion and suggests that Mizelle and Price (1965) had a specimen of *Pygopristis denticulata* before them. Only 1 specimen of 1 (*Pithantheceum piranhus*) of 5 ancyrocephaline species collected and described by Mizelle and Price (1965) was recovered from *P. nattereri* during the present

study. However, 4 of their species, including *C. amazonensis*, *C. piranhus*, *C. serrasalmus*, and *Urocleidus crescentis*, were regularly encountered on *P. denticulata* (nobis, Kritsky et al., in press a). Their fifth species, *Urocleidus orthus*, was apparently not collected, although the possibility exists that *U. orthus* may be a synonym of a species of *Calpidothecioides* described from *P. denticulata* by Kritsky et al. in press a). *Pithantheceum piranhus* and *P. amazonensis* also occur on *Catoprion mento* and *Pristobrycon striolatus*. However, it is unlikely that these host

taxa represent the original fish examined by Mizelle and Price (1965), because 3 of the ancyrocephaline species described by these authors do not occur on these fishes.

Discussion

The Monogenoidea are frequently cited to have a comparatively high host specificity (Llewellyn, 1957; Rhode, 1993). Bychowsky (1957) reported that 711 (74.2%) of 958 known species of Monogenoidea occurred on a single fish species and 806 (84.1%) on species of a single host genus. In a summary of surveys conducted worldwide by various authors, Rohde (1978) found 537 (90.9%) of 591 marine Monogenoidea to occur on members of a single host genus within specific geographic localities. Rohde (1978) related this high host specificity to tendencies for K-strategies of ecological selection. Among other traits, monogenoideans generally produce significantly fewer eggs per individual than members of most other parasitic groups, have a direct life cycle with larval stages actively seeking an appropriate host (Kearn, 1967), and possess complex attachment structures that are frequently specialized to specific sites on hosts (Kearn, 1976).

Since 1984, we have examined 20 species of Serrasalmidae from the Brazilian Amazon for gill parasites (see Boeger and Kritsky, 1988; Kritsky et al., 1992, in press a, b; Van Every and Kritsky, 1992). While diversity of Dactylogyridae on these hosts has been extremely high (about 100 species have been identified), many exhibit low host specificity: *Amphithecium falcatum* occurs on 10 host species; *Notothecium aegidatum* (= *Enallothecium aegidatum*) on 9 host species; *Notozothecium teinodendrum* on 7 host species; *Anacanthorus jegui*, *A. sciponophallus*, *A. mesocondylus*, and *Amphithecium diclonophallum* on 6 host species; and *Notozothecium minor*, *Mymarothecium galeolum*, and *Anacanthorus serrasalmi* on 5 host species each (nobis; Van Every and Kritsky, 1992; Kritsky et al., 1996, in press b). In addition, 2 ancyrocephaline species to be described later (see Kritsky et al. in press b) occur on 8 and 5 hosts, respectively. Of 48 known species of Ancyrocephalinae from serrasalmids, only 21 (43.8%) are known from a single host species, but 23 (47.9%) occur on hosts of 2 or more genera. Expanded studies will undoubtedly show host specificity of these worms to be even lower be-

cause our collections included relatively small numbers of host specimens, all were from a relatively limited geographic area, and many species of serrasalmid hosts have yet to be examined for these parasites in the Neotropical region.

High species diversity is a well-documented phenomenon for a variety of animal and plant groups in the neotropics, and hypotheses have been proposed to explain maintenance of diversity levels and speciation within the region (see Bush, 1994). Although mechanisms of speciation in Neotropical river systems have been discussed less frequently than those for terrestrial systems, the monogenoideans undoubtedly have been exposed and probably responded to the same geologic and paleoecologic events affecting speciation of their fish hosts. Jégu (1992) and Jégu and dos Santos (1993) have suggested that variations in sea level during the glacial and interglacial periods of the Quaternary may have provided many vicariant opportunities for speciation of some fishes including the Serrasalmidae within the Amazon River system. Such reoccurring speciation opportunities coupled with coevolutionary scenarios associated with speciation rates (Brooks, 1979) could explain the high diversity and host occurrences of Dactylogyridae on their Neotropical hosts.

Acknowledgments

The authors are grateful to E. Belmont-Jégu and M. Martins for assistance in the field and to J. R. Lichtenfels (USNPC) and M. H. Pritchard (HWML) for allowing us to examine type and voucher specimens in their care. The Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil, provided accommodations during visits of the senior author to the Amazon Basin. Financial support for this study was provided in part by ISU-FRC (632), ORSTOM, and CNPq. Support of the Brayton H. Ransom Trust Fund for page charges is gratefully acknowledged.

Literature Cited

- Beverley-Burton, M. 1984. Monogenea and Turbellaria. Pages 5–203 in L. Margolis and Z. Kabata, eds. Guide to the Parasites of Fishes of Canada. Part 1. Canadian Special Publication of Fisheries and Aquatic Sciences 74. Department of Fisheries and Oceans, Ottawa, Canada.
- , and D. M. Suriano. 1980. *Cleidodiscus robustus* Mueller, 1934 (Monogenea: Ancyrocephal-

- inae) from *Lepomis gibbosus* L. (Pisces: Centrarchidae) in Ontario, Canada: anatomy and systematic position. *Canadian Journal of Zoology* 58: 654–660.
- Boeger, W. A., and D. C. Kritsky.** 1988. Neotropical Monogenea. 12. Dactylogyridae from *Serrasalminus nattereri* (Cypriniformes, Serrasalminidae) and aspects of their morphologic variation and distribution in the Brazilian Amazon. *Proceedings of the Helminthological Society of Washington* 55: 188–213.
- Brooks, D. R.** 1979. Testing the context and extent of host–parasite coevolution. *Systematic Zoology* 28:299–307.
- Bush, M. B.** 1994. Amazonian speciation: a necessarily complex model. *Journal of Biogeography* 21:5–17.
- Bychowsky, B. E.** 1957. Monogenetic Trematodes, Their Systematics and Phylogeny. The Academy of Sciences of the USSR, Moscow. 509 pp. Translated from Russian by P. C. Oustinoff (W. J. Hargis, Jr., ed.), AIBS, Washington, D.C.
- Jégu, M.** 1992. Influência das alterações climáticas do Quaternário sobre a distribuição e evolução dos peixes na Amazônia. *Proceedings of the 10th Congresso Latino-Americano de Genética*, 21–25 April 1992, Rio de Janeiro. *Revista Brasileira de Genética* 15(supplement 1):234–237.
- , and **G. M. dos Santos.** 1993. Quaternary variation of sea level and present aquatic refuges in central and eastern Amazonia. Page 43 in *Resumos. International Symposium on the Quaternary of Amazonia*, Manaus, Brazil.
- Kearn, G. C.** 1967. Experiments on host-finding and host-specificity in the monogenean skin parasite *Entobdella soleae*. *Parasitology* 57:585–605.
- . 1976. Body surface of fishes. Pages 185–208 (in) C. R. Kennedy, ed. *Ecological Aspects of Parasitology*. North-Holland, Amsterdam.
- Kritsky, D. C., W. A. Boeger, and M. Jégu.** 1996. Neotropical Monogenea. 28. Ancyrocephalinae (Dactylogyridae) of piranha and their relatives (Teleostei, Serrasalminidae) from Brazil and French Guiana: species of *Notothecium* Boeger and Kritsky, 1988, and *Mymarothecium* gen. n. *Journal of the Helminthological Society of Washington*. 63:153–175.
- , ———, and ———. In press a. Neotropical Monogenea. 30. Ancyrocephalinae (Dactylogyridae) of piranha and their relatives (Teleostei, Serrasalminidae) from Brazil: species of *Calpidothecioides* gen. n., *Calpidothecium* gen. n., *Odothecium* gen. n., and *Notothecioides* gen. n. *Journal of the Helminthological Society of Washington*.
- , ———, and ———. In press b. Neotropical Monogenea. 31. Ancyrocephalinae (Dactylogyridae) of piranha and their relatives (Teleostei, Serrasalminidae) from Brazil: species of *Notothecium* Boeger and Kritsky, 1988, and *Enallothecium* gen. n. *Journal of the Helminthological Society of Washington*.
- , ———, and **L. R. Van Every.** 1992. Neotropical Monogenea. 17. *Anacanthorus* Mizelle and Price, 1965 (Dactylogyridae, Anacanthorinae) from characid fishes of the central Amazon. *Journal of the Helminthological Society of Washington* 59:25–51.
- , and **V. E. Thatcher.** 1983. Neotropical Monogenea. 5. Five new species from the aruanã, *Osteoglossum bicirrosus* Vandelli, a freshwater teleost from Brazil, with the proposal of *Gonocleithrum* n. gen. (Dactylogyridae: Ancyrocephalinae). *Proceedings of the Biological Society of Washington* 96:581–597.
- , ———, and **W. A. Boeger.** 1986. Neotropical Monogenea. 8. Revision of *Urocleidoides* (Dactylogyridae, Ancyrocephalinae). *Proceedings of the Helminthological Society of Washington* 53:1–37.
- Llewellyn, J.** 1957. Host-specificity in monogenetic trematodes. Pages 199–212 in *First Symposium on Host Specificity among Parasites of Vertebrates*. Paul Attinger, S.A., Neuchâtel.
- Mizelle, J. D.** 1936. New species of trematodes from the gills of Illinois fishes. *American Midland Naturalist* 17:785–806.
- , and **C. E. Price.** 1963. Additional haptorale hooks in the genus *Dactylogyrus*. *Journal of Parasitology* 49:1028–1029.
- , and ———. 1965. Studies on monogenetic trematodes. XXVIII. Gill parasites of the piranha with the proposal of *Anacanthorus* gen. n. *Journal of Parasitology* 51:30–36.
- Rohde, K.** 1978. Latitudinal differences in host-specificity of marine Monogenea and Digenea. *Marine Biology* 47:125–134.
- . 1993. *Ecology of Marine Parasites*. CAB International, Wallingford, U.K. 298 pp.
- Van Every, L. R., and D. C. Kritsky.** 1992. Neotropical Monogenea. 18. *Anacanthorus* Mizelle and Price, 1965 (Dactylogyridae, Anacanthorinae) of piranha (Characoidea, Serrasalminidae) from the central Amazon, their phylogeny, and aspects of host–parasite coevolution. *Journal of the Helminthological Society of Washington* 59:52–75.